5-2002

Movement Patterns of Phrynosoma mcallii and Phrynosoma platyrhinos in Response to Substrate Texture

Daniel H. Foley III
Utah State University

MOVEMENT PATTERNS OF *PHRYNOSOMA MCALLII* AND *PHRYNOSOMA PLATYRHINOS* IN RESPONSE TO SUBSTRATE TEXTURE

by

Daniel H. Foley III

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Biology

Approved:

Edmund D. Brodie, Jr. Major Professor	Michael E. Pfrender Committee Member
Joseph R. Mendelson III Committee Member	James A. MacMahon Committee Member
Barrie K. Gilbert Committee member	Thomas Kent Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2002

ABSTRACT

Movement Patterns of *Phrynosoma mcallii* and *Phrynosoma platyrhinos* in Response to Substrate Texture

by

Daniel H. Foley III, Doctor of Philosophy

Utah State University, 2002

Major Professor: Dr. Edmund D. Brodie, Jr.
Department: Biology

During the summers of 1999 and 2000 the apparent habitat partitioning of two species of sympatric horned lizards was investigated at the Barry M. Goldwater Bombing Range near Yuma, Arizona. The flat-tailed horned lizard, *Phrynosoma mcallii*, and the desert horned lizard, *P. platyrhinos*, overlap in range in portions of the Sonora desert in the southwestern United States. However, upon finer scale examination, it appeared that these horned lizards were partitioning the available habitat according to soil substrate texture. *Phrynosoma mcallii* appeared to be exclusively found in areas of fine, loose, wind-blown sands, in contrast to *P. platyrhinos*, which appeared to be associated with areas of hardpan substrates covered by small rocks and pebbles. Subsequently, an experiment was set up to test if soil texture was indeed responsible, at least in part, for the observed partitioning of these lizards among the available habitat. Three experimental treatments were established (Sandy, Rocky, Mixed) which differed only with respect to soil texture. Lizards of both species and sexes were fitted with backpacks of thread and

allowed to spool out one pathway in each of the three treatments. Additionally, pathways of *P. mcallii* found on the Naval Air Facility El Centro CA were also collected. This nearby population of *P. mcallii* is allopatric with respect to *P. platyrhinos*. Net displacements, fractal dimensions, and a correlated random walk (CRW) model were utilized to evaluate differences in movement patterns. Similarities in the net displacement and fractal dimension of movement pathways from both species of horned lizards for each of the three treatments suggest substrate composition does not affect species distribution. Additionally, a CRW model severely underpredicted the observed net squared displacement of both *P. mcallii* and *P. platyrhinos* among all three treatments and at both study sites, thus indicating that lizards were moving more linearly than would be expected. Other abiotic factors such as temperature or soil moisture could be important variables in habitat preference. Additionally, due to the sister relationship of these species, phylogenetic constraints in morphology and/or behavior may contribute the to lack of differing movement patterns among varying substrates.

(80 pages)

DEDICATION

This work is dedicated to my wife, Christine. She unselfishly put aside her own personal goals and aspirations to help me achieve mine. For this I will be eternally grateful and I will spend the rest of my life trying to repay her.

ACKNOWLEDGMENTS

I wish to thank the multitude of persons who assisted in making this research possible. First my appreciation goes to my committee, Drs. Brodie, Gilbert, MacMahon, Mendelson, and Pfrender. Particularly, I am grateful to Dr. Brodie for believing in my potential and giving me the opportunity to study under his guidance. Secondly, I would like to thank the department of Navy for providing the necessary funds for this research and their personnel, especially, Brian Morrill, Ron Pearson, Dr. Wylie Homesley, and Patricia Griffin for graciously accommodating my needs while I utilized their facilities. Finally, I wish to thank the field assistants (Jesse Meik, Ty Gardner, Christine Foley, Kevin Young) who helped with data collection, often in the hellish temperatures of a Sonoran summer.

Daniel H. Foley III

CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The study of differences in habitat association among closely related species has long intrigued biologists. Examining patterns of resource use among coexisting species can be valuable for deducing the minimal differences that are compatible with coexistence. Studies of resource partitioning have been very influential in the development of community ecology theory among birds (Robinson and Terborgh, 1995), small mammals (Abramsky and Sellah, 1982; Arlettaz et al., 1997; Glazier and Eckert 2002), amphibians (Hairston, 1980a,b; Morin, 1986), and lizards (Pacala and Roughgarden, 1982, 1985; Petren and Case, 1998; Vitt et al., 1998, 2000).

Interspecific competition is often invoked to explain differences in resource use among sympatric species (MacArthur, 1970; Pacala and Roughgarden, 1982; Losos, 1994). Connell (1961) studied two coexisting species of barnacles in Scotland. His field manipulations demonstrated that competition resulted in the two species occupying different intertidal zones. Hairston (1980a,b; 1987) demonstrated that two coexisting species of salamanders (*Plethodon* spp.), *via* interspecific competition, differed in their pattern of altitudinal distribution. Among lizards (*Anolis* spp.) in the Lesser Antilles, the strength of between-species competition was observed to be inversely related to the degree of interspecific resource partitioning (Pacala and Roughgarden, 1982, 1985).

Interspecific competition is not necessarily static. Weins (1977) suggested that effects of competition on communities are likely to be episodic rather than constant. While investigating desert lizard populations Dunham (1980) found evidence of competition in some years, but not in others. He attributed this temporal variation in competition to variable levels of insect prey that occurred in response to annual variations

in rainfall. Similarly, Smith (1981), also working with desert lizard species, observed evidence of episodic competition. Among his lizard species the strongest evidence for competition came during a time of extreme environmental conditions marked by unusually low rainfall.

Utilization of similar resources by closely related species is of interest to ecologists (Lewin, 1983; Schoener, 1983). Lizards as a group tend to partition resources in three different ways: by being active at different times, by foraging in different places, and by feeding on different prey (James, 1994; Pianka, 1973, 1986; Schoener, 1983). However, among species of whiptail lizards (*Cnemidophorous* spp.) in western North America, all sympatric species were observed to be active during the same time of day, eat similar foods, and possess similar foraging habits (Case, 1979, 1983, 1990; Scudday and Dixon, 1973). Observing that morphologically similar species are more likely to be closely related, Vitt et al. (2000) suggested that similarity in habitats occupied by those species may be phylogenetically constrained. Morphological differences among species may reflect the influence of a combination of ecological factors (i.e., microhabitat use) on the evolution of morphology. Morphological differences were observed to influence habitat use among Caribbean Anoles (Irschick and Losos, 1999). Moreover, character displacement may occur in response to a history of interactions among closely related species resulting in diverging morphologies (Radtkey et al., 1997).

Habitat partitioning may also result if both species respond to varying abiotic factors that differ among microhabitats (Grover, 1996). Differing thermal environments were observed to be an important factor in determining microhabitat selection among lizards occupying Missouri glades (Angert et al., 2002).

Horned lizards (*Phrynosoma* spp.) are restricted to North and Central America. Fourteen morphologically conservative species range from southwestern Canada to Guatemala (Montanucci, 1987; Reeve, 1952). Seven species can be found within the political boundaries of the United States (Stebbins, 1985). The desert horned lizard, *Phrynosoma platyrhinos*, has one of the largest ranges, occurring from southern Idaho and southeastern Oregon southward to northeastern Baja California and northwestern Sonora, Mexico. The flat-tailed horned lizard, *Phrynosoma mcallii*, has one of the most restrictive ranges, occupying a patchy distribution in Yuma County, Arizona (Rorabaugh et al., 1987), and Imperial, Riverside, and San Diego Counties, California (Turner and Medica, 1982) and northeastern Baja California and northwestern Sonora, Mexico (Rorabaugh et al., 1987; Stebbins, 1985; Turner and Medica, 1982). Nearly the entire distribution of *P. mcallii* lies within the distribution of *P. platyrhinos* (Fig. 1) to which it is most closely related (Zamudio and Parra-Olea, 2000).

Phrynosoma mcallii occurs in habitats ranging from fine aeolian sand at the base of dunes to sparsely vegetated gravel flats and mudhills (Beauchamp et al., 1998). Most known localities are below 300 m in elevation (Funk, 1981) and are extremely arid and hot (Norris, 1949). Typical *P. mcallii* habitat consists of loose, sandy hummocks dominated by sparsely distributed creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), and galletta grass (*Hilaria rigida*) with harvester ant mounds present (Rorabaugh et al., 1987; Turner and Medica, 1982).

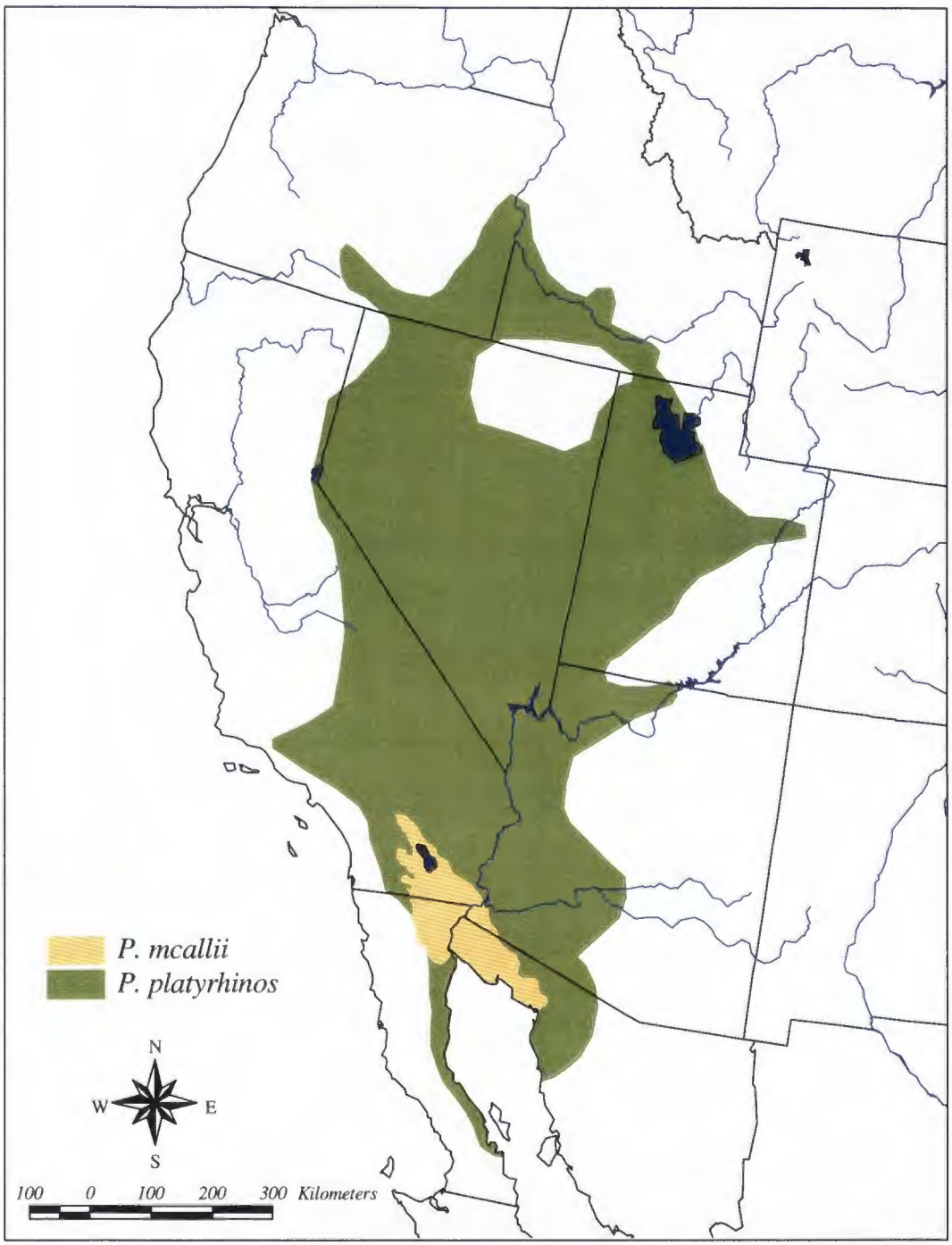

FIG. 1.—Current distribution of *Phrynosoma mcallii* and *Phrynosoma platyrhinos*.

Phrynosoma platyrhinos inhabits arid lands, such as sandy flats, alluvial fans, edges of dunes and along washes. Although this species is often found on hardpan or among gravel, patches of sand are generally present. In the Mojave and Sonoran regions *P. platyrhinos* is associated with creosote bush (*Larrea tridentata*), cactus (*Opuntia* spp.), and ocotillo (*Fouquieria splendens*) and within the Great Basin it is closely associated with sagebrush (*Artemisia* spp.).

The diet of these two species of horned lizards consists of similar prey, primarily ant species (Pianka and Parker, 1975). Moreover, the diet of these lizards in Yuma County, Arizona consists almost entirely of two species of ants, *Pogonomyrmex* spp. and *Messor* spp. (Young, pers. comm.). Also, activity patterns, physiology, and reproductive biology (Howard, 1974) are similar between these two horned lizard species (Young, pers. comm. and pers. obser.).

Movement patterns define the spatial *grain* and *extent* at which organisms are able to interpret habitat structure at a particular scale (Milne, 1997; Wiens, 1990; With, 1994). The perceptual resolution can be inferred by observing how a species responds to the structural complexity of the surrounding habitat. The response of an individual to a heterogeneous landscape will likely be reflected in the pattern of its movement pathway. Assessing species' responses to habitat heterogeneity can be achieved by analysis of movement patterns because they record how and at what scale(s) an individual interacts with habitat structure. Other ecological processes such as predator-prey relationships and population dynamics may be more clearly understood with the knowledge of animal movement patterns with respect to spatial patchiness of a landscape (Johnson et al., 1992; Wiens and Milne, 1989).

Movement is a primary mechanism coupling animals to their environment. Examining animal movement patterns can provide a foundation for understanding broader ecological processes such as home range use (Claussen et al., 1997; Fair and Henke, 1999; Swihart et al., 1988), dispersal behavior (Turchin, 1991), foraging decisions (Anderson, 1983; Bell, 1991; Pyke, 1984), and community interactions (Kareiva and Odell, 1987). The movement patterns of individuals can positively or negatively affect population size, species interaction, or genetic variability. Moreover, because the actual movement path and the environment through which the track passes are recorded, we can test mechanistic hypotheses about the environmental cues that may affect movement. However, to understand the possible practical importance of any of these processes, we need to quantify movement patterns, and understand how spatial heterogeneity and distribution of conspecifics may enhance or reduce individual animal movement patterns.

Movement pathways are often quite complex. Environmental structure may play an important role in dictating movement pathways and therefore may indicate how different species perceive habitat heterogeneity. On the Barry M. Goldwater bombing range (BMGR), approximately 25 km southwest of Yuma, Arizona, *Phynosoma mcallii* and *P. platyrhinos* occur in sympatry with respect to each other. Both of these species are known to have similar activity patterns and rely on the same prey base for the majority of their diets. Differences in microhabitat characteristics, on the other hand, may be a variable whereby these species are able to coexist. The occurrence of these two lizard species on the BMGR appears to indicate a correlation between substrate texture and prevalence of a particular horned lizard species (Fig. 2). *Phynosoma mcallii* appears

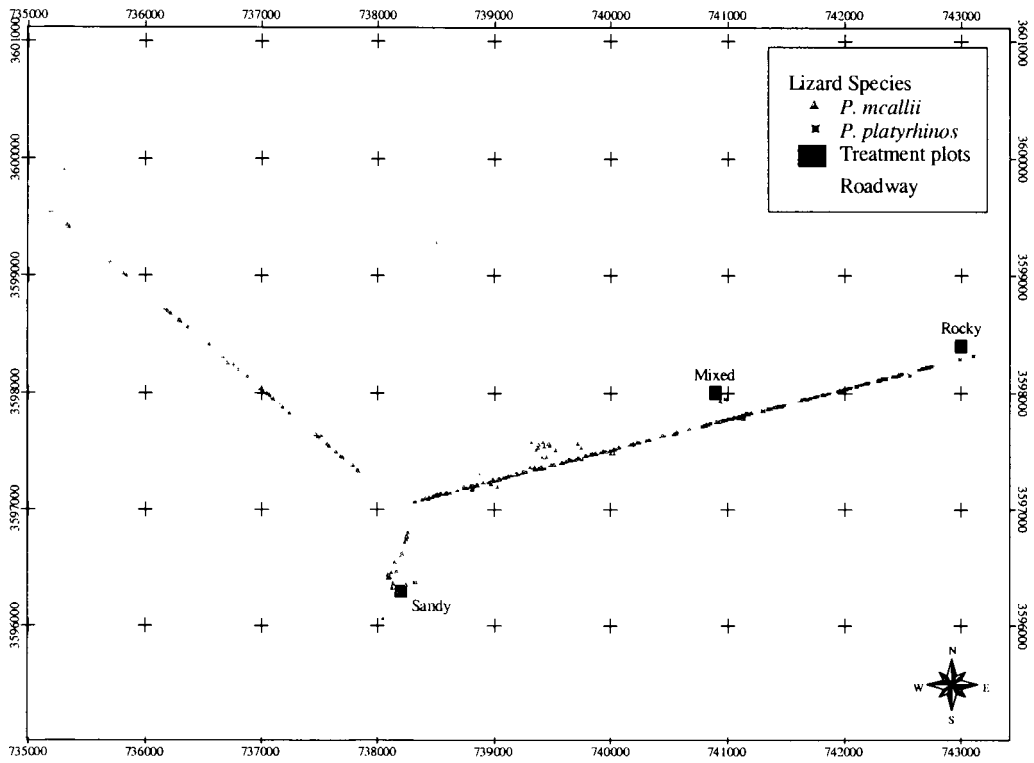

FIG. 2.—Location of treatment plots and *Phrynosoma mcallii* and *P. platyrhinos* observations during 1999.

to associate more closely with fine, loose, wind-blown sand and *P. platyrhinos* with harder, compact, hard-pan substrate. By analyzing individual movement patterns of both species, I hope to gain insight into the importance of substrate texture as an important variable influencing the distribution of these horned lizard species on the BMGR.

My hypothesis is that *P. mcallii* and *P. platyrhinos* are partitioning the landscape according to microhabitat preferences. More specifically I predict that *P. mcallii* prefers a substrate consisting of fine, wind blown sands, and *P. platyrhinos* prefers a substrate

consisting of more compact, hard-pan substrate. Soil texture has been observed to influence the distribution of desert seed-harvester ants (Johnson, 1992). Moreover, harvester ants have been shown to greatly influence community and ecosystem structure (MacMahon et al., 2000). To address my central hypothesis, I will address whether the movement patterns of *P. mcallii* and *P. platyrhinos* differ between areas of varying substrate texture. To evaluate differences in movement patterns between species, among varying substrates, three differing indices of movement patterns were used. The simplest of these is the lizards' net displacement, the straight-line distance traveled from start point to end point relative to the actual distance traveled. It is assumed that lizards that interpret an available habitat as sub-optimum should attempt to exit that habitat as quickly as possible, resulting in large straight-line displacements. Conversely, it is assumed that those lizards that interpret a habitat as satisfactory will not want to exit a habitat as quickly and should possess more convoluted pathways and therefore smaller straight-line displacements. Perhaps a more rigorous way of testing the relationship between horned lizard species distribution and soil substrate texture is to analyze lizard movement paths relative to a correlated random walk (CRW) model (Bergman et al., 2000; Kareiva and Shigesada, 1983; McCulloch and Cain, 1989; Root and Kareiva, 1984). The CRW model predicts that an individual's net squared displacement will grow linearly as the individual takes successive steps (Turchin, 1998). Therefore, the movement pathways of those lizards that perceive available habitat as satisfactory should approach those predicted by the CRW model. Conversely, those lizards that perceive habitat as sub-optimum should have net squared displacements significantly greter than that predicted by a CRW model.

The distance an individual moves may simply be a function of the size of the animal. Species of differing size often move at different rates and therefore trace differing pathways (Peters, 1983). Comparisons among organisms are necessarily complicated by this scale-dependence of movement patterns. The fractal dimension of a pathway is independent of scale, measuring the tortuosity of that pathway. Analysis of the fractal dimension of animal movement pathways therefore offers an objective method of inferring an individual's perception of spatial heterogeneity across a range of scales (Dicke and Burrough, 1988; Milne, 1991). Analysis of the fractal dimension of movement patterns from different species within the same landscape may therefore reveal insights on how different species perceive landscape structure (Wiens et al., 1995) Differences in fractal dimensions between species among similar habitats suggest that each species interprets the landscape differently (i.e., at different scales) and may partition the landscape accordingly. The fractal dimension of pathways may provide a useful measure for comparing habitat selection of differing taxa.

In a population located at the Naval Air Facility (NAF) El Centro, California, *P. mcallii* occurs allopatrically with respect to *P. platyrhinos*. This population of lizards will be used to address whether the movement patterns of *Phrynosoma mcallii* differ in areas where it occurs sympatrically and allopatrically with respect to *P. platyrhinos*.

MATERIALS AND METHODS

Study Areas

Two study areas were utilized over the course of two field seasons. One site, located in southern California, represents an area in which *P. mcallii* is allopatric with respect to *P. platyrhinos*. Specifically, this study site was located in the Imperial Valley of Imperial County on the Naval Air Facility property approximately 20 km from El Centro, California. From May to August of 2000, 25 *P. mcallii* (10 female; 15 male) were utilized to record movement patterns of each lizard at its original site of capture. These represent pathways observed from lizards in "familiar" habitat. The soil substrate at NAF El Centro consists of fine, wind-blown sandy soil. Throughout the landscape the sandy soil has coalesced into a thin "skin" of a brittle sandstone-like surface over a fine sandy subsurface. Human foot traffic easily breaks through this sandstone skin, revealing soft sand underneath. The resulting landscape is a mosaic of small wind-blown sand dunes and bare hard-pack sand substrate. Plant communities on the NAF El Centro are very homogeneous, consisting almost entirely of creosote bush (*Larrea tridentata*) scrub (Fig. 3A). Although creosote is the most common shrub throughout the majority of the NAF El Centro, white bursage (*Ambrosia dumosa*) is occasionally codominant in some areas and is sometimes more dominant than creosote in other areas. A 28-year record of climatic conditions indicate an average July temperature of 32.8 C and an average annual precipitation of 6.17 cm per year (U.S. Dept. of Ag., 1941).

The second site, located on the Barry M. Goldwater Bombing Range (BMGR) in extreme southwestern Arizona, Yuma County, represents an area where *P. mcallii* and *P.*

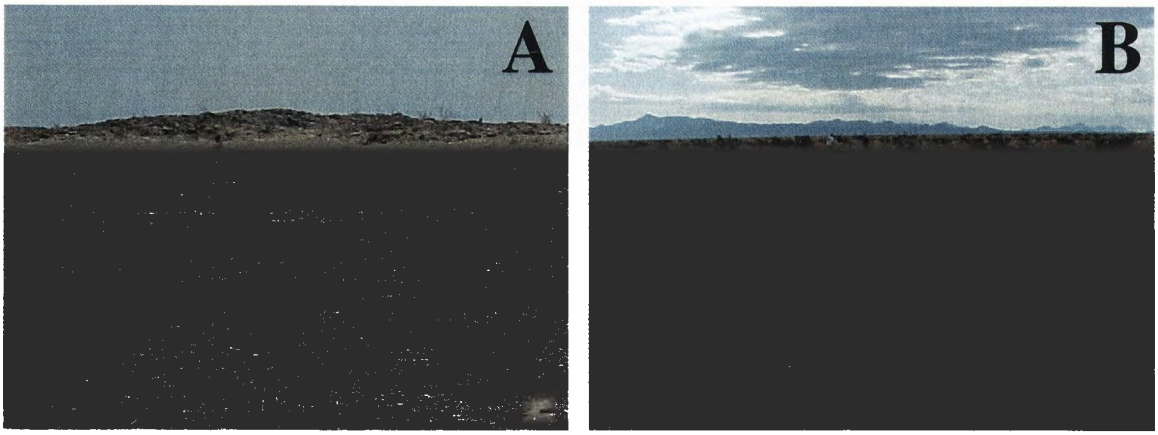

FIG. 3.—Typical plant communities at (A) NAF El Centro and (B) BMGR.

platyrhinos occur sympatrically. A single paved road on the BMGR extends east from County 19th road in Yuma, past "Aux II" (a simulated aircraft carrier training facility), and continues to "Yodaville" (a simulated small town, used for aircraft bombing training). A field station and living quarters (UTM 743000 3598400) were adjacent to this road approximately 20 km from the County 19th entrance on to the BMGR. The field station marks the southeastern boundary of the study area. From May to August of 1999, pathways of 22 *P. mcallii* (11 female; 11 male) and 22 *P. platyrhinos* (11 female; 11 male) were recorded in three treatments differing in substrate texture. From May to August 2000, pathways of 25 *P. platyrhinos* (10 female; 15 males) were observed to record movement patterns of each lizard at its original site of capture.

The substrate on the BMGR makes a transition along a gently sloping elevation gradient from hard-packed substrate with gravel and coarse sand in the east (~120 m elevation) to loose sandy hummocks in the west (~90 m elevation). The distribution of *P. mcallii* and *P. platyrhinos* within the study area approximately follows this transition

with *P. mcallii* occurring on the more western sandy soils and *P. platyrhinos* occurring on the more eastern rockier soils, with some overlap in both species along a transitional zone (Fig. 2). This transitional zone between substrates and between species intersects the road at approximately 110 m elevation around UTM 741000 3597500. The primary vegetation over the whole study area consists of sparsely distributed creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), and galletta grass (*Hilaria rigida*) (Fig. 3B). A 40-year record of climatic conditions indicate an average July temperature of 32.8 C and an average annual precipitation of 9.09 cm per year (U.S. Dept. of Ag., 1941).

During the 1999 field season, three experimental 1-hectare plots were located in the field on the BMGR. Each plot was selected based on differences only with respect to substrate texture. One plot's substrate consisted entirely of fine wind-blown sand, and shall from this point on be referred to as "Sandy" (Fig. 4A). The second plot's substrate

FIG. 4.—*Phrynosoma platyrhinos* on "Sandy" (A) and *P. mcallii* on "Rocky" soil substrates (B).

consisted entirely of hardpan soil covered by a thin layer of small pebbles and shall from this point on be referred to as "Rocky" (Fig. 4B). The third plot's substrate possessed a mosaic pattern of the previous Sandy and Rocky substrates in approximately equal proportions and shall from this point on be referred to as "Mixed."

Collection of Lizards Pathways

In order to collect individual lizard pathways, a modification of a spool and thread backpack design was utilized (Fisher and Muth, 1995; Wilson, 1994). Cocoon bobbins of thread (~90 m in length) were encased in small rectangles of nylon. Natural-colored nylon stockings were cut into rectangles approximately 40 mm wide by 60 mm long. A cocoon bobbin of thread, each approximately 32 mm long and 1.0 g in weight, was positioned in the middle of the nylon rectangle. The nylon was then folded over and stretched tightly so that the cocoon bobbin was positioned along the fold of the nylon. The two side seams of the nylon packet were then sealed with heat from a pocket cigarette lighter. Care was taken when sealing the seams, as too much heat would cause excessive melting of the nylon. Two small openings, one on each side of the packet adjacent to the fold, were left unsealed. The outward tag end of the cocoon bobbin was tied to the nylon at one opening and the other inner tag end was allowed to free spool out the other opening. Then with sharp scissors, the bottom portion of the seam along each side of the packet was trimmed, resulting in two tabs of nylon that could be spread apart at 180° from each other. These tabs then allowed for surfaces to which the nylon packet could be glued to the backs of the lizards (Fig. 5). Each nylon packet of thread typically represented less than 10% of each lizard's body weight. A thin film of 100% silicon

glue was spread on the back of each lizard with a toothpick. The nylon packet of thread was then positioned by laying the two tabs onto the glue on the lizard's back. The lizards, with newly attached nylon packets of thread, were placed in holding containers with sand, to allow the glue to dry. Often the lizards would bury themselves in the sand allowing sand to also adhere to the glue, facilitating additional camouflage for the lizard (Fig. 6). Usually within an hour or two, the glue was dry to the touch.

Upon release of each lizard, a survey flag was positioned at the start point and the loose inner tag end of the bobbin was tied to the flag. All lizards were released in the evening just at dusk. As horned lizards are strictly diurnal (Heath, 1965; Pianka and Parker, 1975), this allowed for each lizard to sleep near the point of release and acclimate to the local surroundings. At dawn the following morning each lizard then spooled out the contents of its bobbin of thread. Status of each lizard was checked hourly after sunrise until the lizard had spooled out the entire contents of its bobbin. If the lizard was scheduled to record another pathway in another treatment, the lizard was recollected and another backpack of thread was attached. The lizard was then released that same

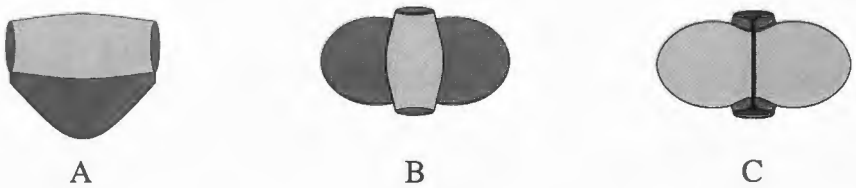

FIG. 5.—Diagram of nylon backpack design. (A) Lateral view. (B) Top view. (C) Bottom view.

FIG. 6.—*Phrynosoma mcallii* with attached nylon packet of thread.

evening in the appropriate treatment. After each lizard's data collection was complete, it was released at its original point of capture and subjected to no further harassment.

During the 1999 field season, one pathway within each of the three treatment plots was collected from each lizard. During the 2000 field season, one pathway was collected from each lizard at the BMGR and NAF El Centro study sites. These lizards were not translocated to treatment plots and pathways were collected from the location of original capture for each lizard.

Each lizard's pathway was surveyed and mapped with a Trimble Pathfinder® Pro XRS real-time differential G.P.S. unit (approximately 50 cm precision). Position locations were recorded at 1-second intervals while slowly walking over the lizards pathway. Distances between consecutive positions therefore corresponded approximately to my stride length. The resulting step length (distance between two consecutive points) was approximately 40–50 cm. The subsequent coordinate data were used to generate

pathway maps. Real-time differential postprocessing was achieved through a subscription with the independent satellite company, OmniStar.

Data Analysis

In order to compare the movement patterns of lizards between treatments and study sites, analysis of the movement pathways were quantified using three differing techniques.

Net Displacement

The simplest method used was to examine the net displacement of lizard pathways. Net displacement is simply defined as the straight line distance an individual moved from start point to end point. Program FRACTAL (Nams, 1996) was utilized to calculate the straight-line distance of each pathway. Data collected from both species of horned lizards during the 1999 field season were analyzed with a three-way factorial ANOVA design. This procedure tested for differences in the net displacement among species, gender, and three treatment plots.

Data gathered on pathways of *P. mcallii* during the 2000 field season were analyzed with a two-factor ANOVA. This procedure tested for differences in lizard pathways of *P. mcallii* in the net displacement between the two study sites. Tests for normality were performed and the data transformed if necessary. Significance was determined at $\alpha = 0.05$.

Fractal Dimension

The fractal dimension (D) of a movement pathway may provide a scale-independent measure of how landscape structure affects movement. The fractal dimension of horned lizard pathways was computed by the dividers method (Dicke and Burrough, 1988; Milne, 1991) which involves measuring the total length of a pathway using varying "ruler" lengths. As the length of the ruler used to measure the pathway increases, the total length of the pathway decreases since more of the detail in the pathway is ignored. Thirty ruler lengths were used to measure the length of each lizard's pathway. The regression of the natural log of the total path on the natural log of the ruler length results in a slope, which when subtracted from 1 yields D. This relationship can be summarized as:

$$L(\delta) = k\delta^{1-D}$$

where L is the length of the pathway, δ is the length of the ruler used to measure the pathway, k is the intercept of the regression line, and D is the fractal dimension. Among two-dimensional pathways, D can theoretically range from 1–2. A value of 1.00 would indicate a straight line and a value of 2.00 would indicate a pattern which was so convoluted that it completely filled a plane (Mandelbrot, 1983). In practice, values of D for movement pathways will range between these extremes, and therefore indexes the tortuosity of movement (With, 1994). Program FRACTAL (Nams, 1996), a fractal analysis software package, was utilized to calculate the fractal dimension of each pathway.

Data collected from both species of horned lizards during the 1999 field season were analyzed with a three-way factorial ANOVA design. This procedure tested for differences in the fractal dimensions among species, gender, and three treatment plots. Data gathered on pathways of *P. mcallii* during the 2000 field season were analyzed with a two-factor ANOVA. This tested for differences in lizard pathways of *P. mcallii* in fractal dimension between the two study sites. Tests for normality were performed and fractal dimensions were corrected with a LOG(n – 1) transformation. Significance was determined at $\alpha = 0.05$.

Correlated Random Walk

Correlated random walk (CRW) models can be used to make comparisons of movement behaviors in different habitats (McCulloch and Cain, 1989). The effects of landscape heterogeneity can be evaluated by comparing observed net squared displacements of movement pathways to those predicted by a CRW model. Net squared displacements are informative because they show a linear relationship with increasing steps or time (Turchin, 1998). For each path, the distances and angles between successive locations are recorded. The distribution of these variables is utilized to make predictions of net squared displacement using the correlated random walk model of Kareiva and Shigesada (1983):

$$\overline{R}_n^2 = nm_2 + 2m_1 \frac{\varphi}{1-\varphi}\left(n - \frac{1-\varphi^n}{1-\varphi}\right)$$

where $\overline{R}_n^2$ is the expected net squared displacement, n is the step number, m_1 is the mean move length, m_2 is the mean squared move length, and φ is the average cosine of the turning angle.

For my horned lizard data, predicted net squared displacements were compared with observed displacements. Linear regression was used to estimate the slope of the relationship between predicted and observed net squared displacement and number of successive steps. A *t*-test (Zar, 1999) was used to test for significant differences between the observed and expected slopes. Significance was determined at $\alpha = 0.05$.

RESULTS

1999 Field Season

During the summer of 1999, 22 adult individuals of *P. mcallii* (11 of each sex) (Table 1) and 22 adult individuals *P. platyrhinos* (11 of each sex) (Table 2) were captured and morphometric data (SVL, weight) collected. One pathway was collected from each lizard in each of three treatment plots (Sandy, Mixed, Rocky) resulting in 132 total pathways collected.

To evaluate quantitative differences in soil substrate texture between the three treatments, soil penetrometer recordings were taken from each treatment. A penetrometer is used to evaluate the soils compressive strength. Measurements were

TABLE 1.—1999 morphometric data of those Yuma, AZ *Phrynosoma mcallii* from whom pathways were collected.

Females			Males		
Id No.	SVL (mm)	Weight (g)	Id No.	SVL (mm)	Weight (g)
8104	74.5	17.45	9055	63.8	10.37
9049	66.6	15.60	9060	64.5	12.28
9067	69.0	13.28	9061	60.3	11.07
9079	67.9	13.25	9062	70.1	14.50
9080	74.6	20.70	9063	73.2	14.41
9082	67.9	11.95	9088	75.7	15.08
9105	72.6	14.66	9090	70.4	15.25
9116	75.4	14.99	9091	65.6	13.16
9118	72.2	14.15	9119	72.8	15.51
9210	72.6	16.36	9164	71.5	14.27
9241	68.6	10.43	9227	75.0	13.99
Mean	71.1	14.75		69.3	13.63

TABLE 2.—1999 morphometric data of those Yuma, AZ *Phrynosoma platyrhinos* from whom pathways were collected.

Females			Males		
Id No.	SVL (mm)	Weight (g)	Id No.	SVL (mm)	Weight (g)
9019	70.5	20.88	8081	73.1	17.61
9047	71.0	15.18	9050	70.0	16.16
9052	74.5	18.75	9053	80.9	24.34
9059	73.1	15.88	9124	75.4	18.40
9066	73.3	17.93	9126	78.5	19.51
9078	75.1	17.79	9187	75.0	17.31
9081	75.4	17.66	9188	77.2	23.83
9096	71.9	13.78	9194	--	--
9099	79.8	19.72	9213	79.5	21.11
9161	81.2	18.96	9216	85.0	21.91
9181	78.1	16.30	9233	76.9	18.76
Mean	74.9	17.53		77.2	19.89

taken at 16 locations evenly distributed across each treatment. The average penetrometer reading among the Sandy, Mixed, and Rocky treatments were 0.148 kg/cm^2 (SE = 0.016), 0.179 kg/cm^2 (SE = 0.021) and 1.388 kg/cm^2 (SE = 0.182), respectively. Significant differences in soil strength were observed between the three treatment plots ($F_{2,45}$ = 44.54; $P < 0.001$). Further post hoc tests indicated that the soils strength of the Sandy ($P < 0.001$) and Mixed ($P < 0.001$) treatments were significantly less than the Rocky treatment.

Net Displacement

During the summer of 1999 the 11 *P. mcallii*, females traveled an average net displacement of 51.5 m, 44.6 m, and 45.0 m among the Rocky, Mixed, and Sandy plots,

respectively. By comparison, the 11 *P. mcallii* males traveled an average 43.3 m, 49.3 m, and 49.9 m among the Rocky, Mixed, and Sandy plots, respectively. Alternatively, 11 *P. platyrhinos* females traveled an average net displacement of 60.5 m, 51.8 m, and 48.5 m among the Rocky, Mixed, and Sandy plots, respectively, while the 11 *P. platyrhinos* males traveled and average net displacement of 49.4 m, 53.5 m, and 54.8 m among the Rocky, Mixed, and Sandy plots, respectively (Fig. 7). No significant differences were observed in the net displacement between either female or male *P. mcallii* and female or male *P. platyrhinos* ($F_{3,40} = 1.46$, $P = 0.241$) or between the interaction of either species and sex and treatment ($F_{6,80} = 1.17$, $P = 0.328$).

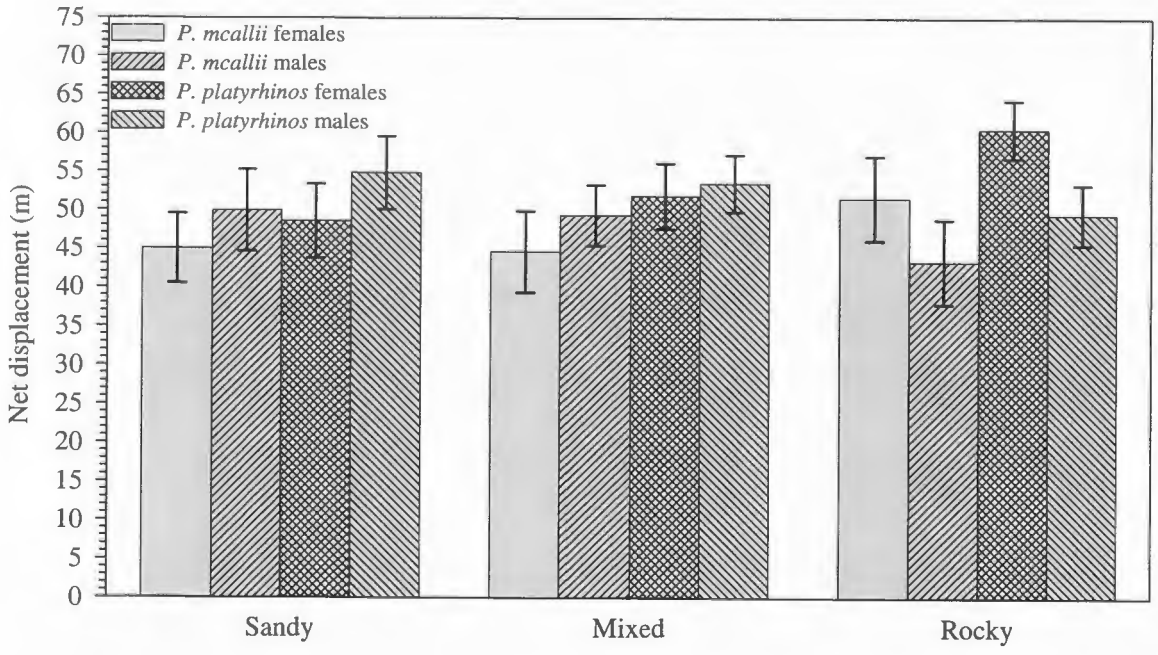

FIG. 7.—Average net displacement of 22 *P. mcallii* and 22 *P. platyrhinos* (11 females and 11 males of each species) among three treatment plots in Yuma, Arizona. Error bars equal ± 1 SE.

Correlated Rrandom Walk

The pathways of same lizard species and sex were averaged together within each of the three treatments during the 1999 field season. For each of three treatments, net displacements of *Phrynosoma mcallii* females were not well described by a CRW model. In each case, Sandy ($t = 41.20$; $df = 414$; $P < 0.001$), Mixed ($t = 49.25$; $df = 428$; $P < 0.001$), and Rocky ($t = 37.29$; $df = 418$; $P < 0.001$), the CRW model significantly under-predicted the observed displacement (Figs. 8–10). Breaks along each observed displacement graph occur due to few individuals achieving the corresponding number of consecutive steps.

For *P. mcallii* males, the same trend was observed. For each of three treatments, net displacements were not well described by a CRW model (Figs. 11–13). In each case, Sandy ($t = 47.40$; $df = 466$; $P < 0.001$), Mixed ($t = 48.75$; $df = 488$; $P < 0.001$), and Rocky ($t = 25.79$; $df = 460$; $P < 0.001$), the CRW model significantly underpredicted the observed displacement.

For female *Phrynosoma platyrhinos* pathways, for each of three treatments, net displacements were not well described by a CRW model (Figs. 14–16). In each case, Sandy ($t = 24.67$; $df = 440$; $P < 0.001$), Mixed ($t = 33.51$; $df = 448$; $P < 0.001$), and Rocky ($t = 37.40$; $df = 440$; $P < 0.001$), the CRW model significantly underpredicted the observed displacement.

For *P. platyrhinos* males, the same trend was observed only for the Sandy and Mixed treatment plots. For these two treatments, net displacements were not well described by a CRW model (Figs. 17–18). In each case, Sandy ($t = 38.51$; $df = 458$; $P < 0.001$), Mixed ($t = 58.21$; $df = 448$; $P < 0.001$), the CRW model significantly under

predicted the observed displacement. However, those 11 *P. platyrhinos* male pathways within the Rocky treatment did move as expected according to a CRW model ($t = 1.92$; $df = 490$; $0.10 > P > 0.05$) (Fig. 19).

Fractal Dimension

During the summer of 1999 the 11 *P. mcallii* female pathways had an average fractal dimension of 1.0585, 1.0774, and 1.0796 among the Rocky, Mixed, and Sandy plots, respectively. The 11 *P. mcallii* male pathways had an average fractal dimension of 1.0746, 1.0797, and 1.0791 among the Rocky, Mixed, and Sandy plots, respectively. In comparison, the 11 *P. platyrhinos* female pathways had an average fractal dimension of 1.0387, 1.0609, and 1.0702 among the Rocky, Mixed, and Sandy plots, respectively, and the 11 *P. platyrhinos* male pathways had an average fractal dimension of 1.0640, 1.0671, and 1.0620 among the Rocky, Mixed, and Sandy plots, respectively (Fig. 20). An initial ANOVA indicated no significant differences in average fractal dimension among both horned lizard species and sex and any of the treatments ($F_{6,80} = 1.63$, $P = 0.149$). However, *a posteriori* tests indicated that the average fractal dimension of *P. platyrhinos* females within the Rocky treatment was significantly smaller than *P. mcallii* females within the Sandy treatment ($P = 0.046$) and *P. mcallii* males from the Mixed treatment ($P = 0.033$).

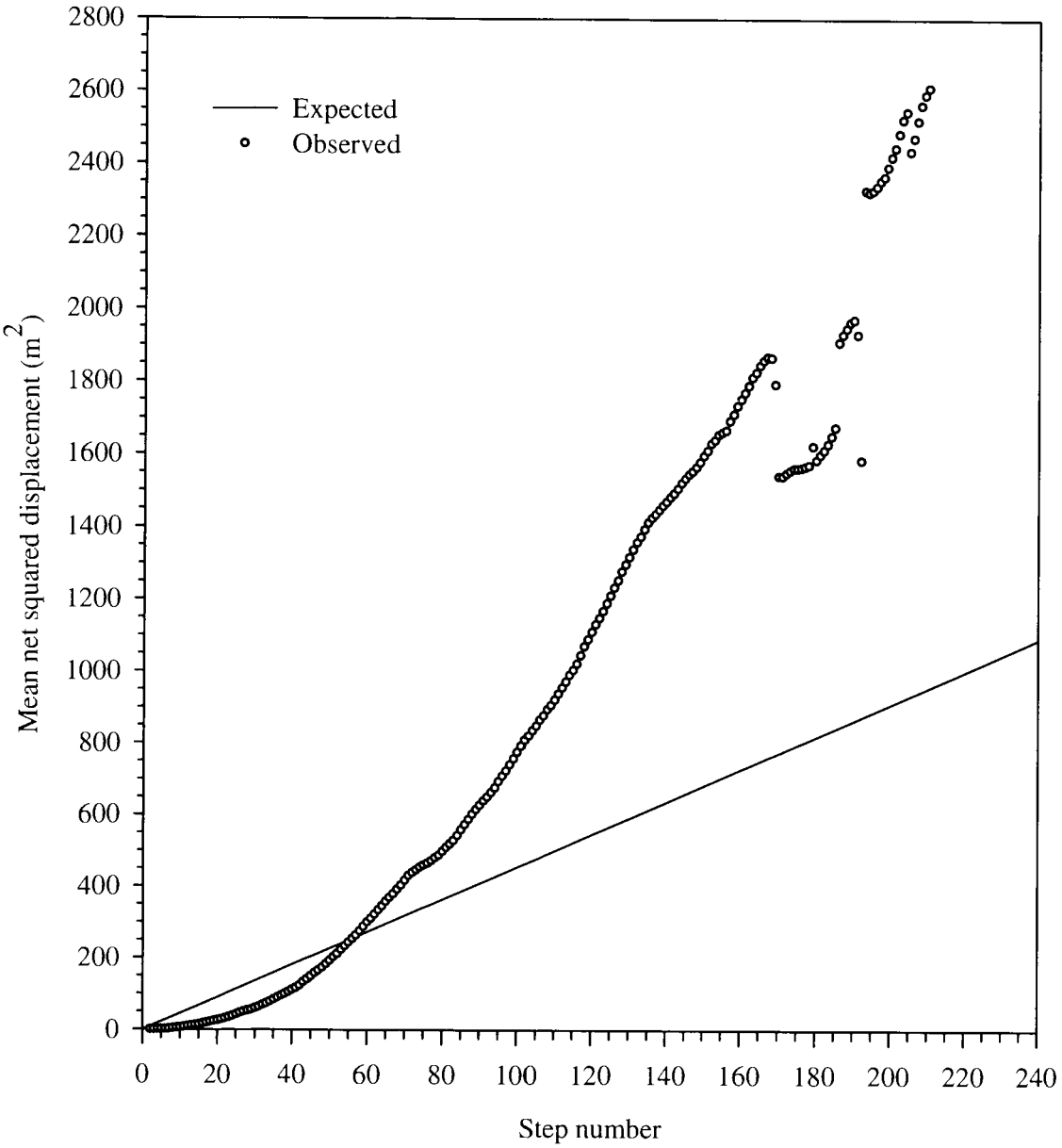

FIG. 8.—Observed (symbols) and predicted (solid line) mean net squared displacement of 11 female *Phrynosoma mcallii* within the Sandy treatment on the BMGR, near Yuma, AZ during the summer of 1999.

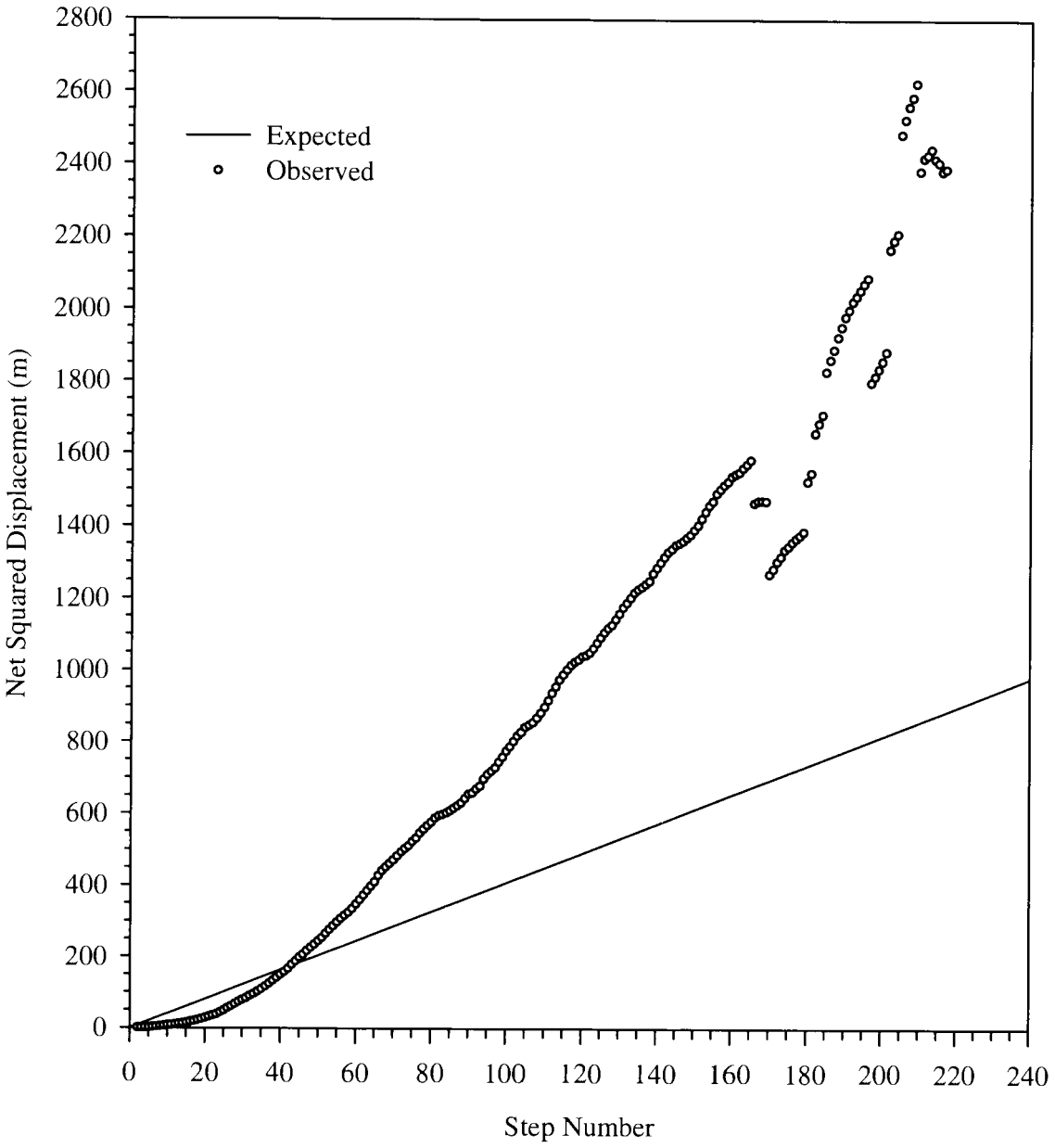

FIG. 9.—Observed (symbols) and predicted (solid line) mean net squared displacement of 11 female *Phrynosoma mcallii* within the Mixed treatment on the BMGR, near Yuma, AZ during the summer of 1999.

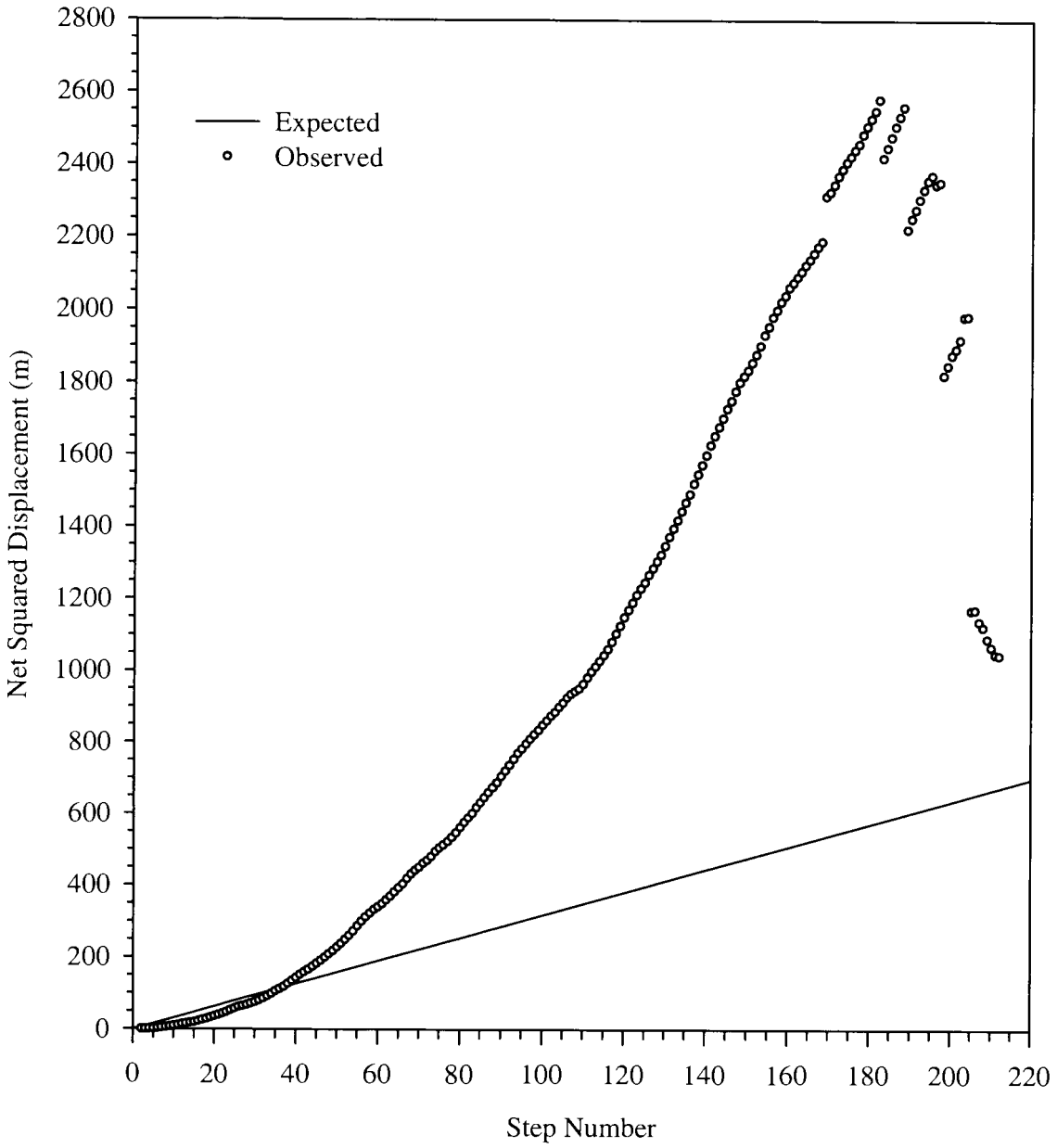

FIG. 10.—Observed (symbols) and predicted (solid line) mean net squared displacement of 11 female *Phrynosoma mcallii* within the Rocky treatment on the BMGR, near Yuma, AZ during the summer of 1999.

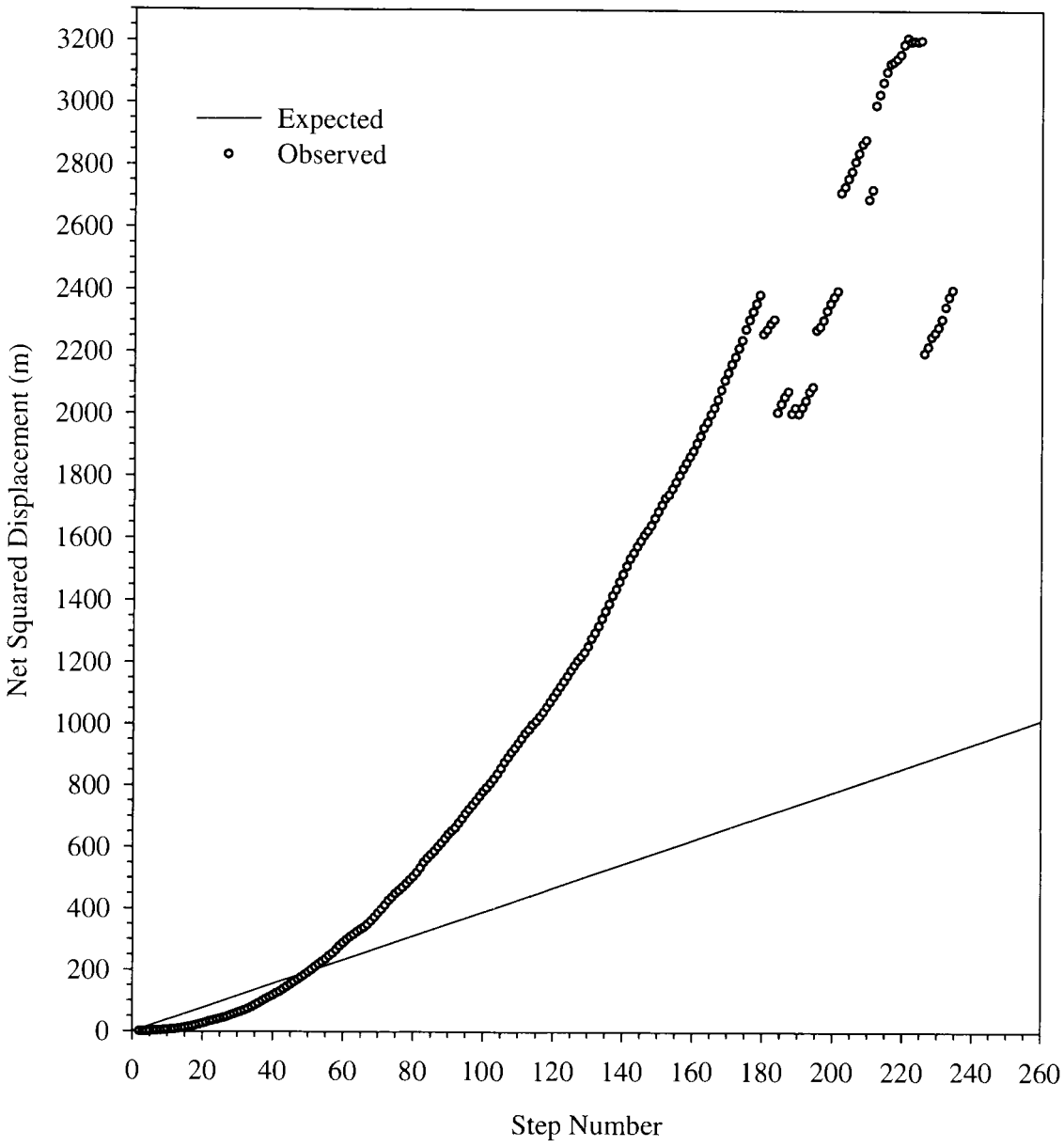

FIG. 11.—Observed (symbols) and predicted (solid line) mean net squared displacement of 11 male *Phrynosoma mcallii* within the Sandy treatment on the BMGR, near Yuma, AZ during the summer of 1999.

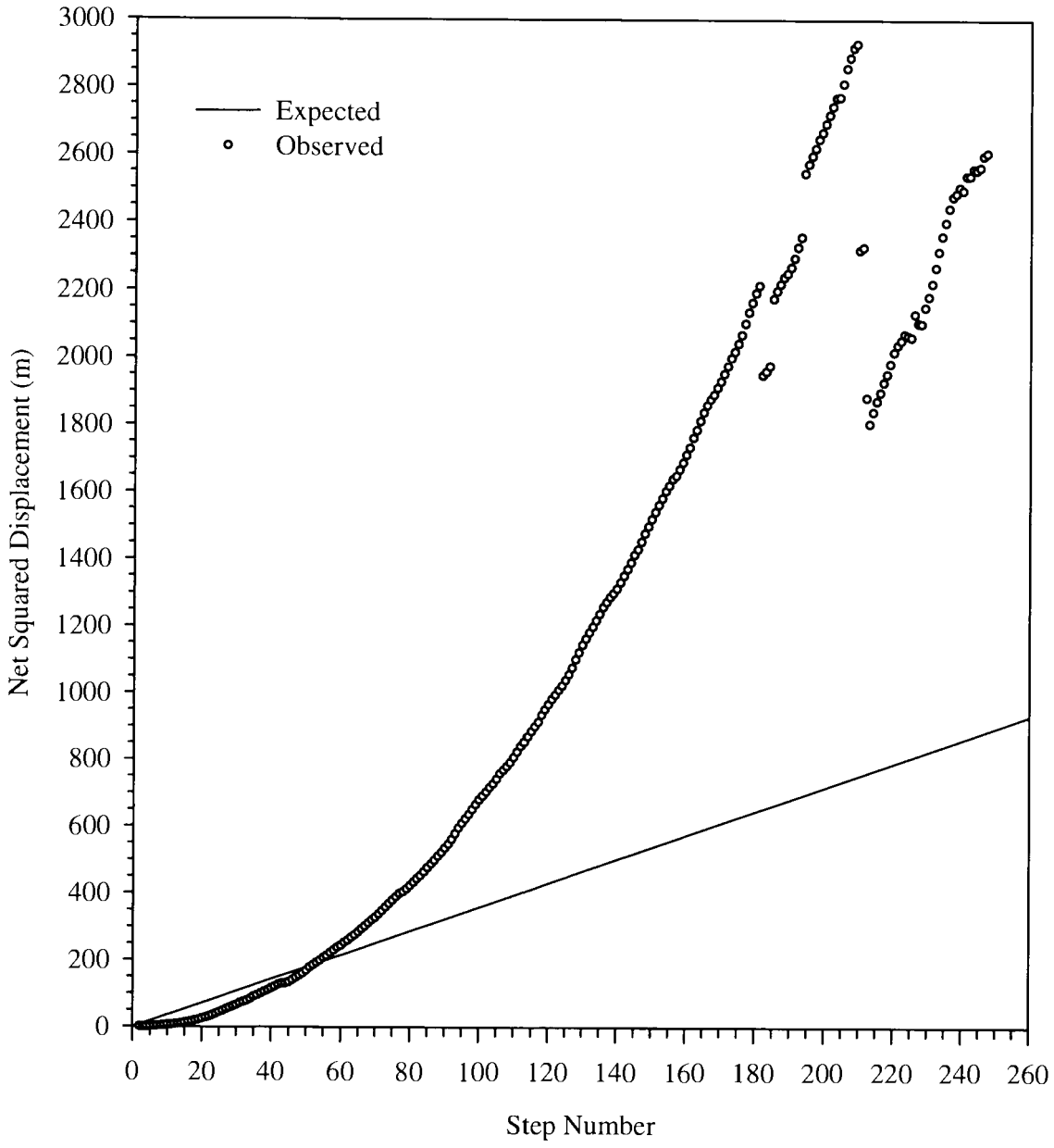

FIG. 12.—Observed (symbols) and predicted (solid line) mean net squared displacement of 11 male *Phrynosoma mcallii* within the Mixed treatment on the BMGR, near Yuma, AZ during the summer of 1999.

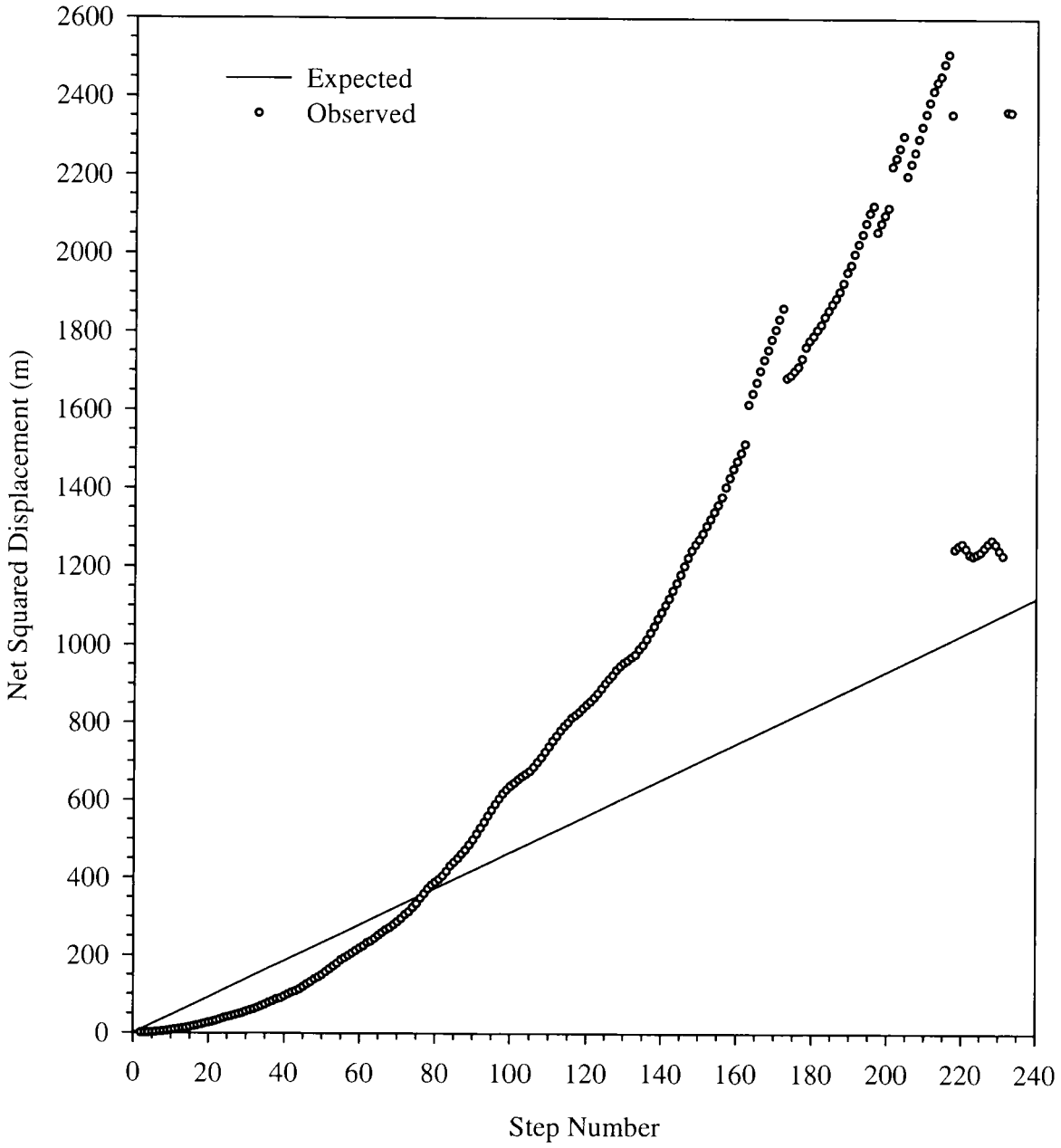

FIG. 13.—Observed (symbols) and predicted (solid line) mean net squared displacement of 11 male *Phrynosoma mcallii* within the Rocky treatment on the BMGR, near Yuma, AZ during the summer of 1999.

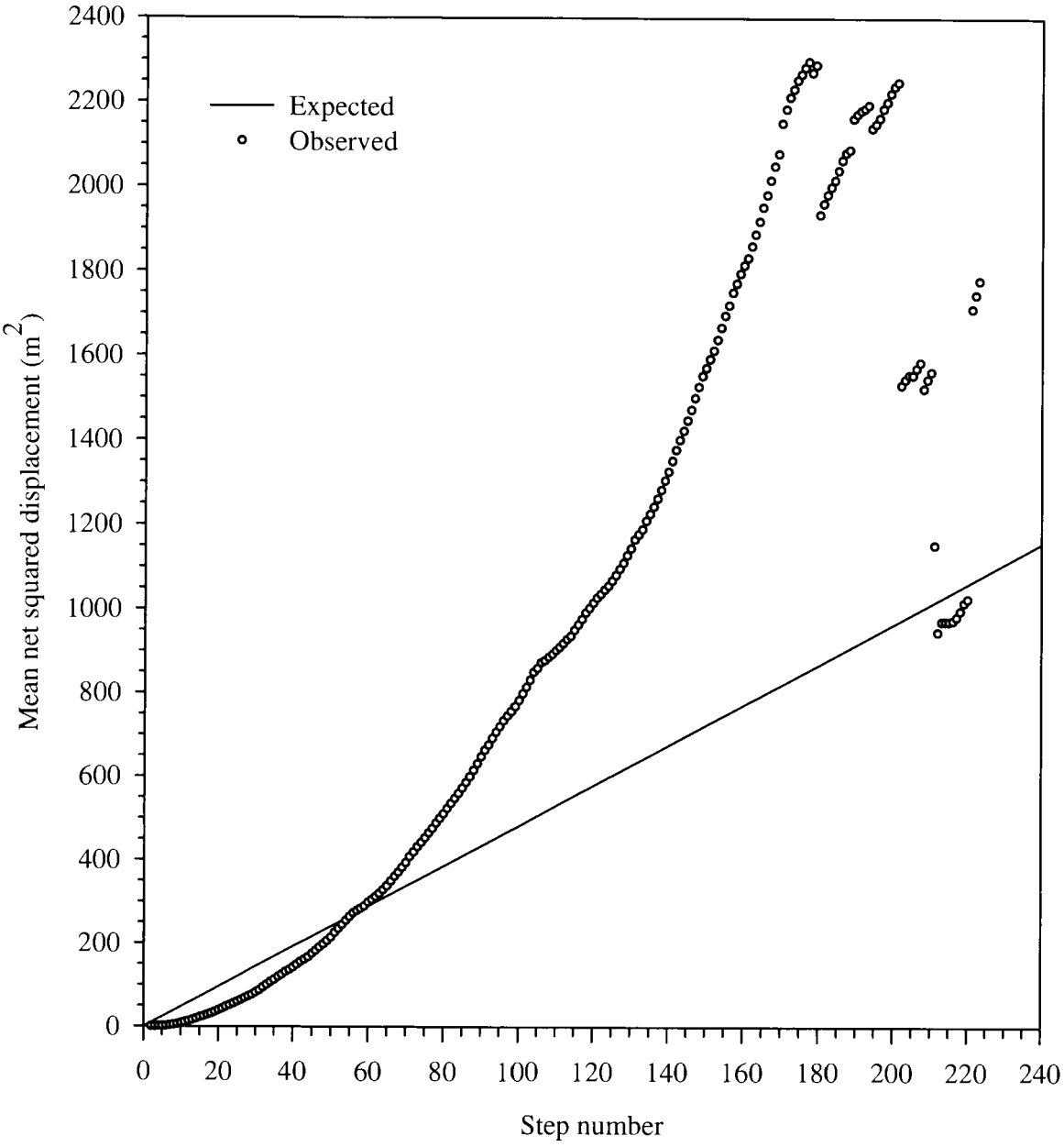

FIG. 14.—Observed (symbols) and predicted (solid line) mean net squared displacement of 11 female *Phrynosoma platyrhinos* within the Sandy treatment on the BMGR, near Yuma, AZ during the summer of 1999.

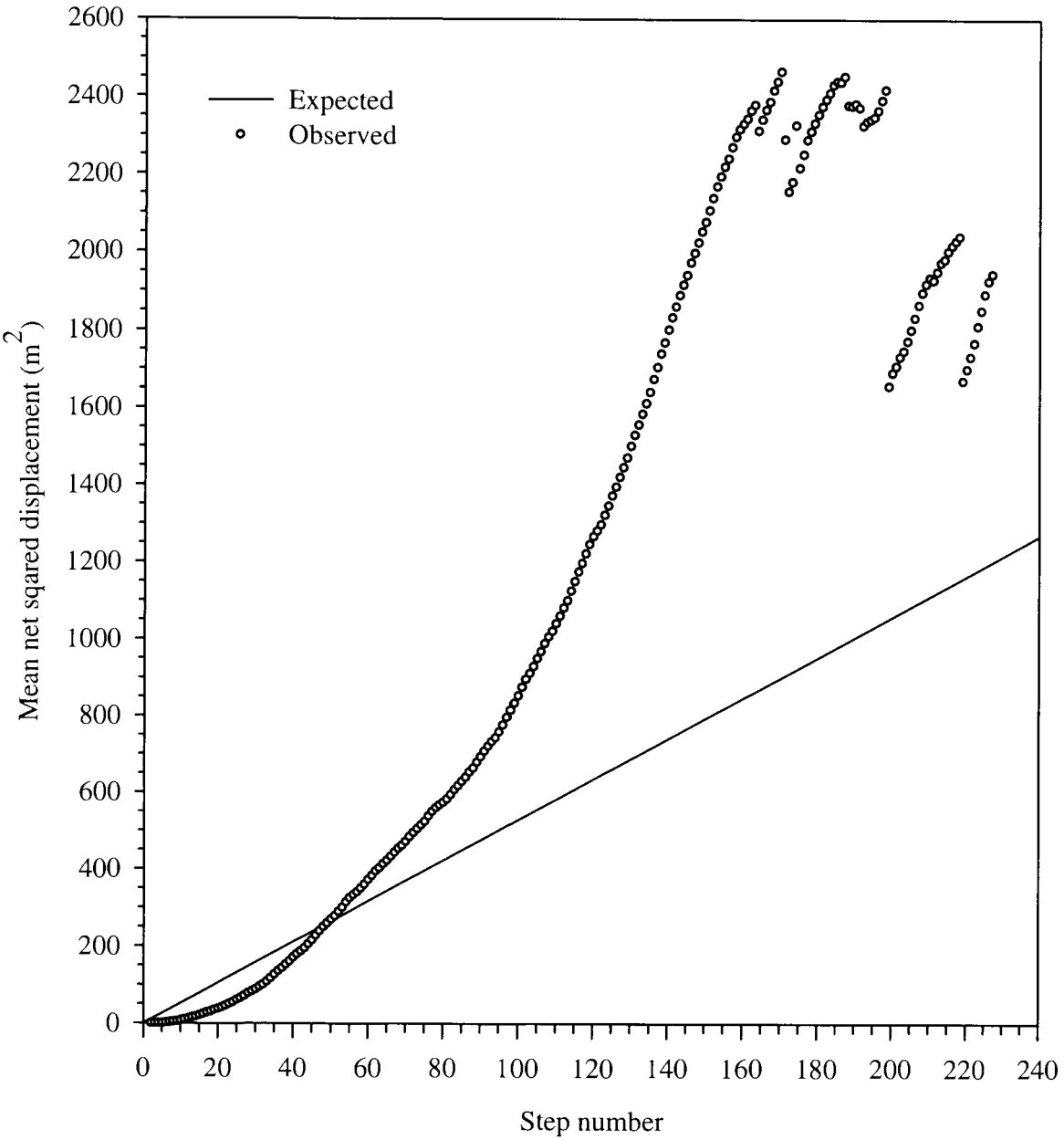

FIG. 15.—Observed (symbols) and predicted (solid line) mean net squared displacement of 11 female *Phrynosoma platyrhinos* within the Mixed treatment on the BMGR, near Yuma, AZ during the summer of 1999.

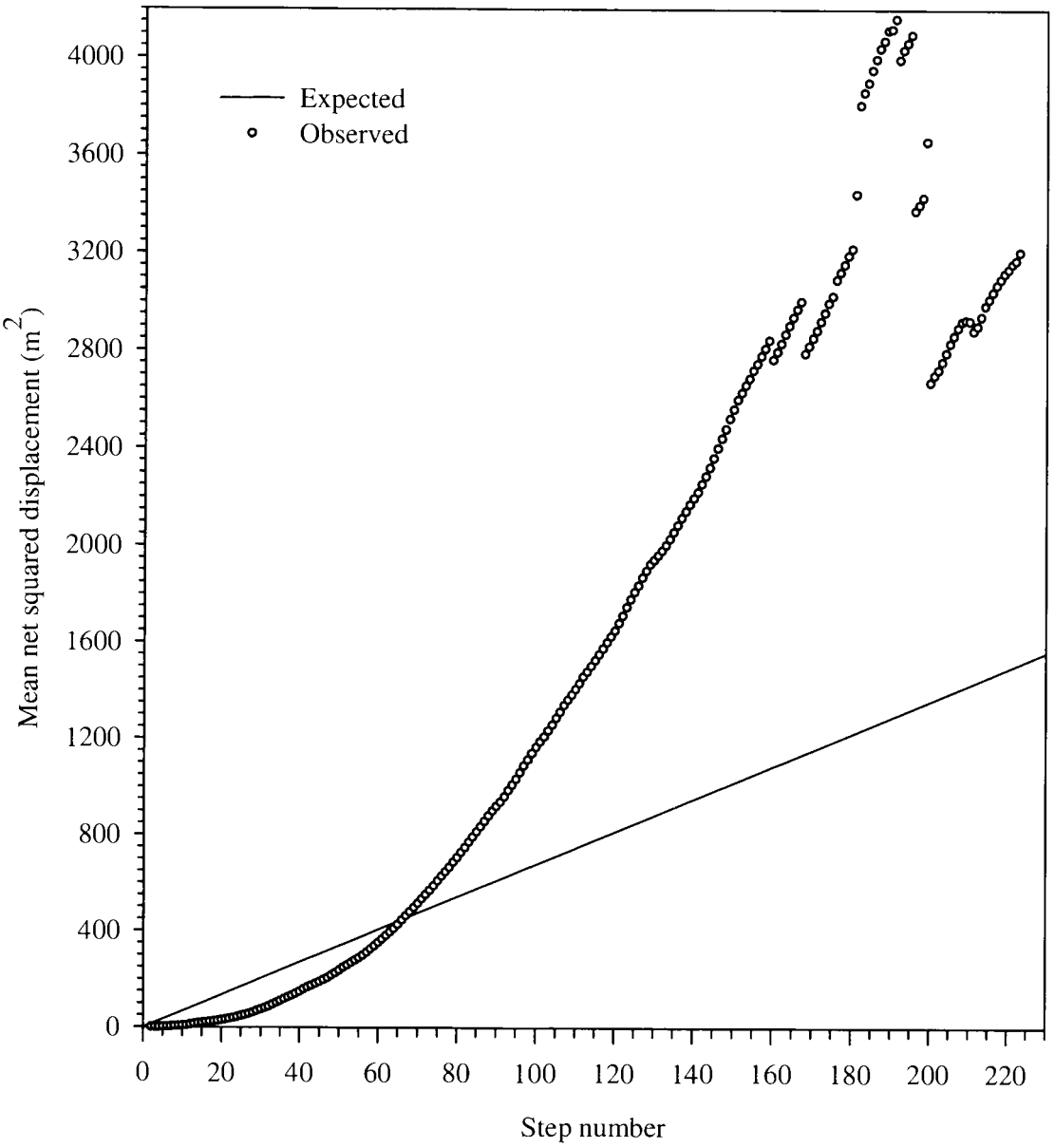

FIG. 16.—Observed (symbols) and predicted (solid line) mean net squared displacement of 11 female *Phrynosoma platyrhinos* within the Rocky treatment on the BMGR, near Yuma, AZ during the summer of 1999.

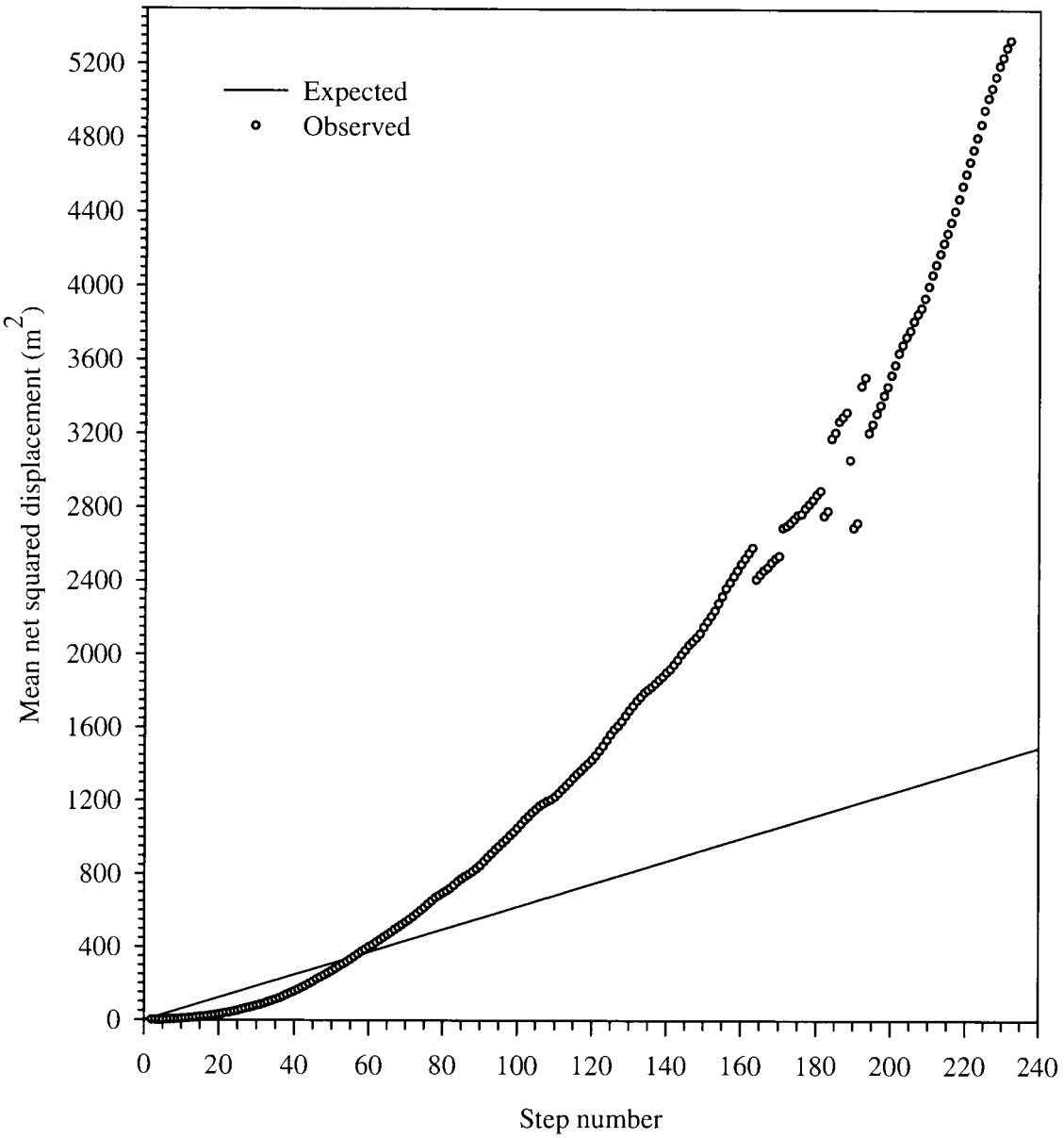

FIG. 17.—Observed (symbols) and predicted (solid line) mean net squared displacement of 11 male *Phrynosoma platyrhinos* within the Sandy treatment on the BMGR, near Yuma, AZ during the summer of 1999.

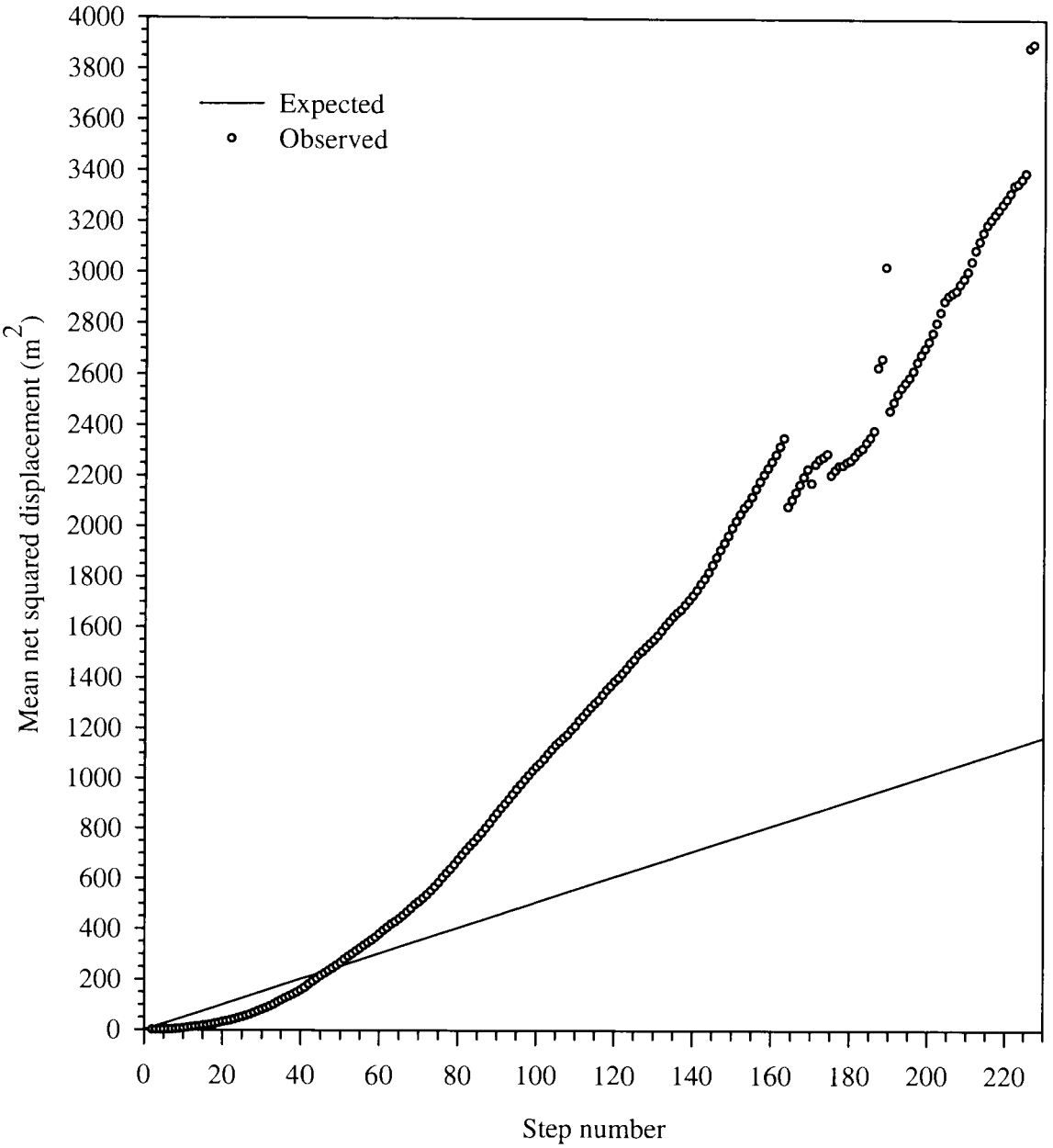

FIG. 18.—Observed (symbols) and predicted (solid line) mean net squared displacement of 11 male *Phrynosoma platyrhinos* within the Mixed treatment on the BMGR, near Yuma, AZ during the summer of 1999.

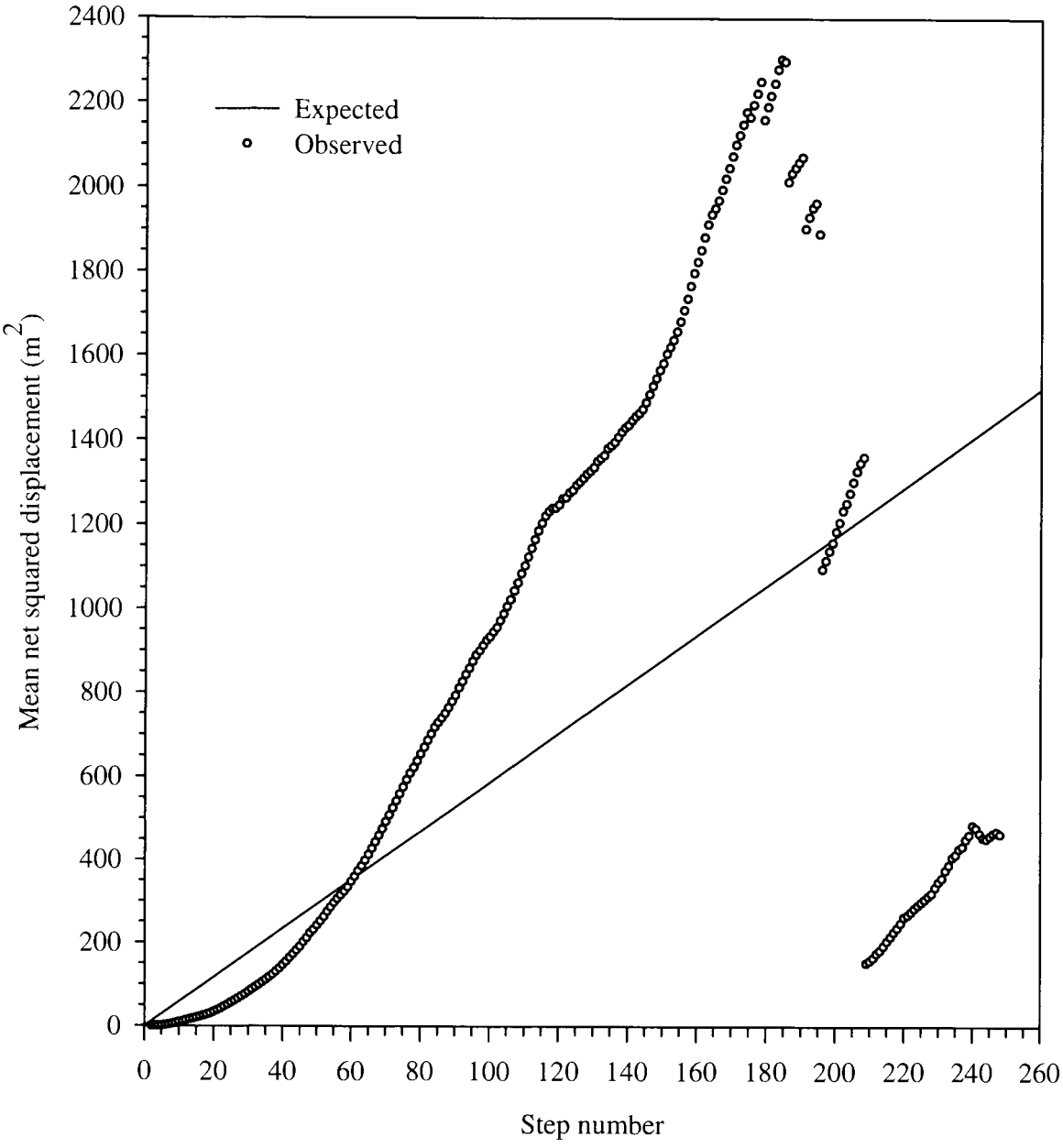

FIG. 19.—Observed (symbols) and predicted (solid line) mean net squared displacement of 11 male *Phrynosoma platyrhinos* within the Rocky treatment on the BMGR, near Yuma, AZ during the summer of 1999.

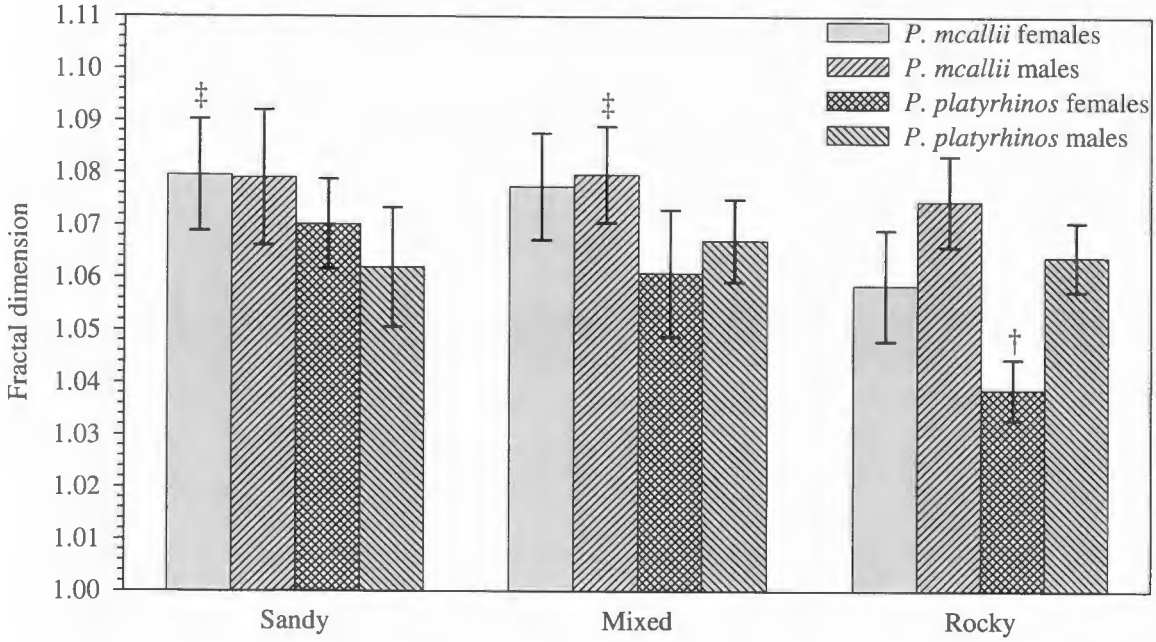

Fig. 20.—Average fractal dimension of 22 *P. mcallii* and 22 *P. platyrhinos* (11 females and 11 males of each species) pathways among three treatment plots in Yuma Arizona. Error bars equal ± 1 SE. Bars with different symbols denote significant differences ($P < 0.05$) in mean fractal dimensions.

2000 Field Season

During the summer of 2000, 25 additional *P. mcallii* pathways, one from each of 10 females and 15 males, were collected from the Yuma, Arizona study BMGR site (Table 3). Also during the summer of 2000, one pathway from each of 25 individual *P. mcallii* (10 females; 15 males) was collected from the NAF El Centro, CA study site (Table 4). Those pathways collected during the 2000 field season were recorded from individuals at their original site of capture. These individuals were not translocated to each of the three treatment plots utilized during 1999. Each of these lizards was allowed to spool out one bobbin of thread from their site of capture.

TABLE 3.—2000 morphometric data of those Yuma, AZ *Phrynosoma mcallii*, from whom pathways were collected.

Females			Males		
Id No.	SVL (mm)	Weight (g)	Id No.	SVL (mm)	Weight (g)
0002	64.1	9.09	0003	69.2	12.34
0039	62.2	10.70	0035	75.9	16.24
0052	72.0	14.35	0040	71.6	13.28
0097	76.3	11.87	0041	71.1	14.57
0099	71.4	9.86	0048	73.3	14.33
0120	71.0	10.08	0053	76.6	15.67
0124	65.7	10.43	0074	70.2	11.15
0126	67.8	11.72	0077	67.2	9.31
0128	68.6	11.04	0090	65.8	9.74
0162	70.0	12.85	0094	67.0	9.47
			0100	66.7	12.64
			0104	64.4	10.68
			6300	70.6	13.35
			9098	75.1	14.59
			9130	73.6	12.14
Mean	68.9	11.20		70.5	12.63

Net Displacement

The 10 female *P. mcallii* captured on the BMGR during 2000 traveled an average net displacement of 35.1 m and the 15 male *P. mcallii* traveled an average net displacement of 44.4 m. The 10 female *P. mcallii* captured on the NAF El Centro during 2000 had an average net displacement of 39.4 m and the 15 males had an average net displacement of 47.6 m (Fig. 21). The average net displacement of *P. mcallii* (males and females collectively) from BMGR and NAF El Centro did not differ ($F_{1,50} = 0.62$; $P = 0.437$). Moreover, neither males nor females from BMGR differed in average net

TABLE 4.—2000 morphometric data of those El Centro, CA *Phrynosoma mcallii*, from whom pathways were collected.

Females			Males		
Id No.	SVL (mm)	Weight (g)	Id No.	SVL (mm)	Weight (g)
D07	71.7	14.96	D02	59.0	7.77
D08	77.8	21.08	D06	74.5	15.04
D24	80.7	18.94	D09	68.1	13.13
D25	76.5	14.90	D10	79.0	21.45
T01	73.5	18.02	D15	78.1	16.11
T03	66.0	12.11	D16	76.9	16.00
T11	72.5	13.43	D17	74.3	17.14
T14	82.9	22.85	D18	67.9	9.87
T17	71.3	15.52	D19	71.7	16.28
T18	73.2	13.05	D20	67.1	11.88
			D21	68.7	12.08
			D22	76.8	15.86
			T12	65.4	9.41
			T13	81.1	17.22
			T16	59.5	9.74
Mean	74.6	16.49		71.2	13.93

displacement from males or females from NAF El Centro ($F_{1,50} = 0.01$; $P = 0.914$).

The average net displacements of *P. mcallii* male and female pathways recorded at their original site of capture (BMGR and NAF El Centro 2000) were compared to pathways of *P. mcallii* which were translocated to plots of differing substrate texture (Rocky, Mixed, Sandy). No significant difference in average net displacements of *P. mcallii* pathways within each of the three BMGR treatment plots during 1999 and BMGR and NAF El Centro in 2000 were observed ($F_{4,112} = 0.72$; $P = 0.582$) (Fig. 22).

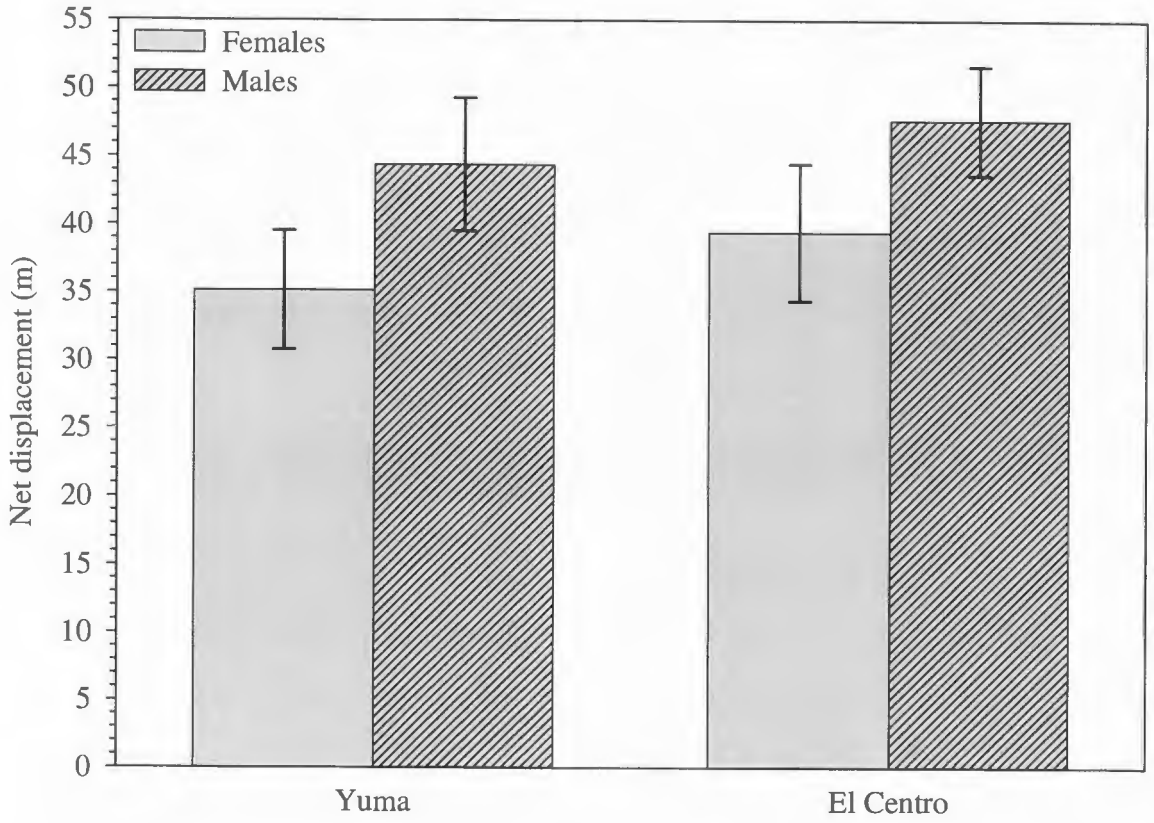

FIG. 21.—Average net displacement of 25 (10 female;15 male) Yuma and 25 (10 females; 15 males) El Centro *P. mcallii* pathways collected during the 2000 field season. Error bars equal ± 1 SE.

Correlated Random Walk

The pathways of same lizard species and sex were averaged together for each study site during the 2000 field season. Among the 25 *P. mcallii* pathways observed on the NAF El Centro during 2000, neither the females' (t = -11.65; df = 440; $P < 0.001$) (Fig. 23) nor the males' (t = 13.19; df = 360; $P < 0.001$) (Fig. 24) movement patterns were well described by a CRW model. For the 25 *P. mcallii* observed on the BMGR during 2000, neither the females' (t = 10.18; df = 376; $P < 0.001$) (Fig. 25) nor the males'

(t = -2.57; df = 394; $P < 0.01$) (Fig. 26) movement patterns were well described by a CRW model.

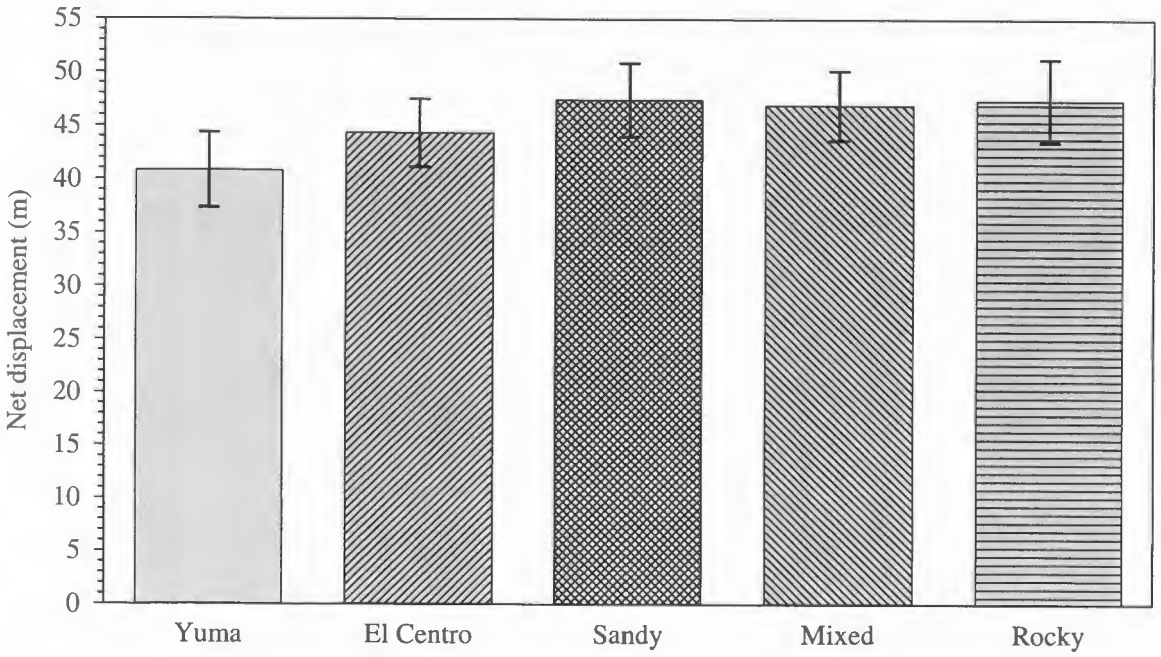

FIG. 22.—Average net displacement of combined female and male *P. mcallii* pathways collected during the 1999 and 2000 field season. Error bars equal ± 1 SE.

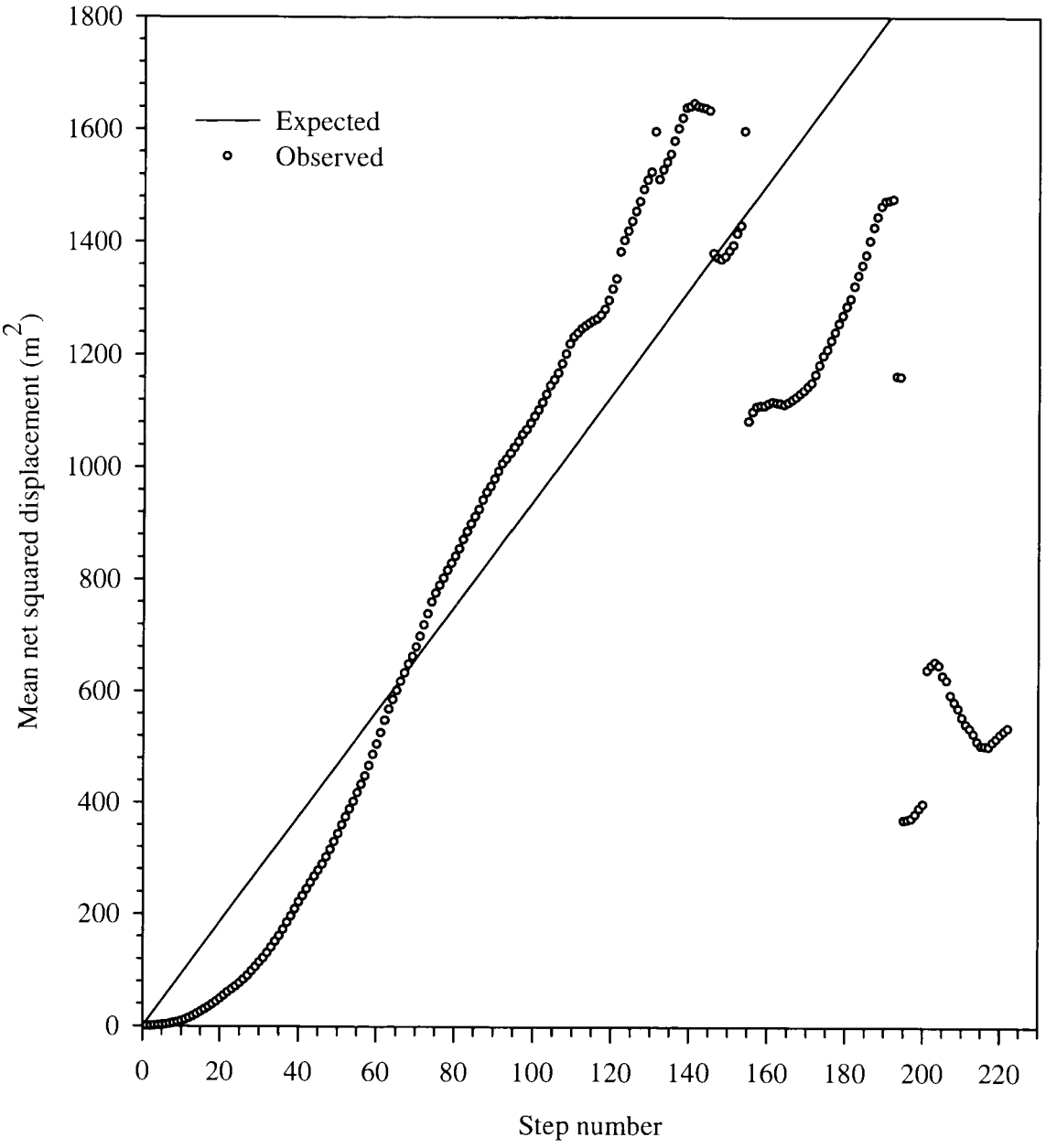

FIG. 23.—Observed (symbols) and predicted (solid line) mean net squared displacement of 10 female *Phrynosoma mcallii* pathways collected on the Naval Air Facility, near El Centro, CA, during the summer of 2000.

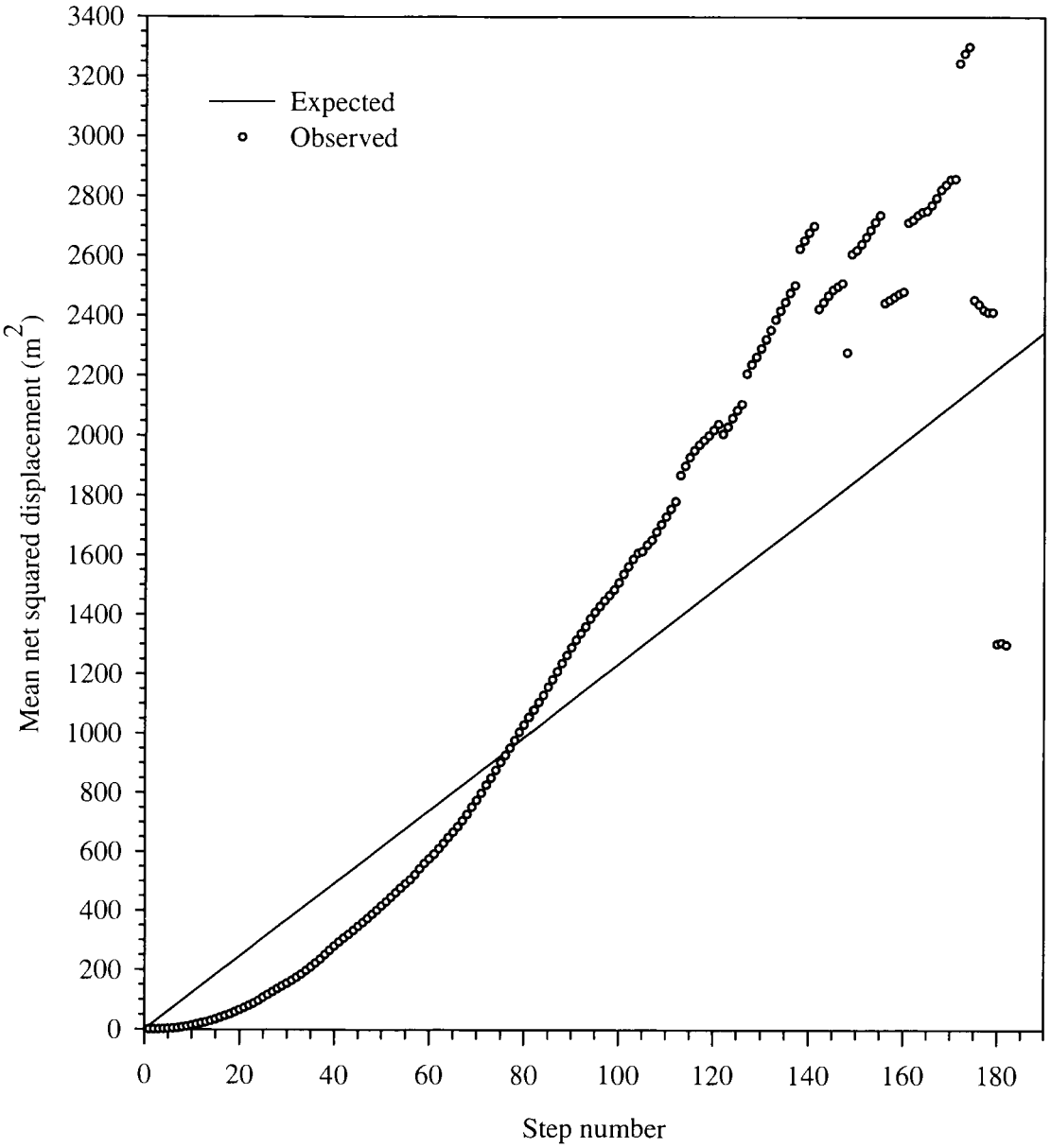

FIG. 24.—Observed (symbols) and predicted (solid line) mean net squared displacement of 15 male *Phrynosoma mcallii* pathways collected on the Naval Air Facility, near El Centro, CA, during the summer of 2000.

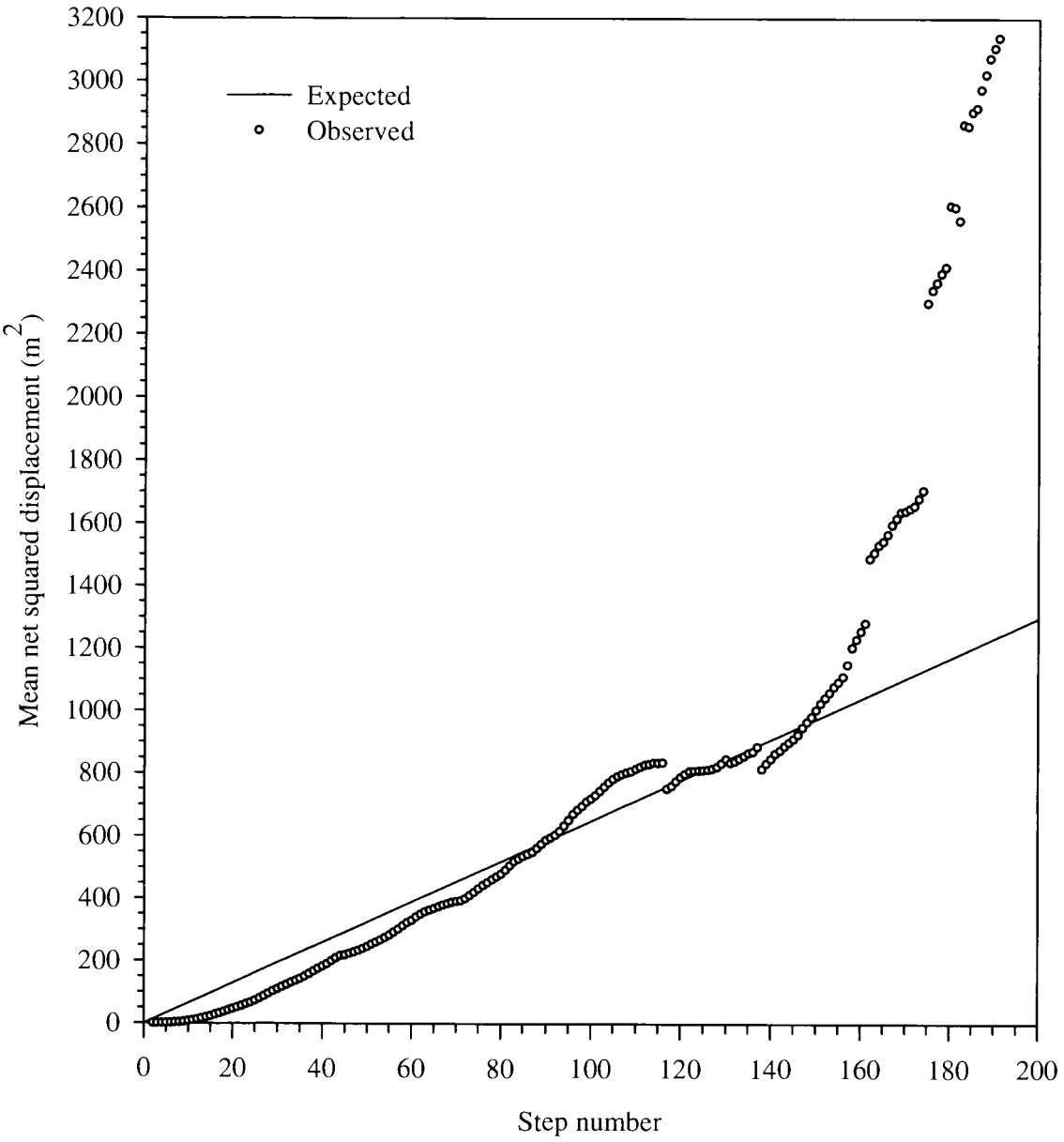

FIG. 25.—Observed (symbols) and predicted (solid line) mean net squared displacement of 10 female *Phrynosoma mcallii* pathways collected on the Barry M. Goldwater bombing range, near Yuma, AZ, during the summer of 2000.

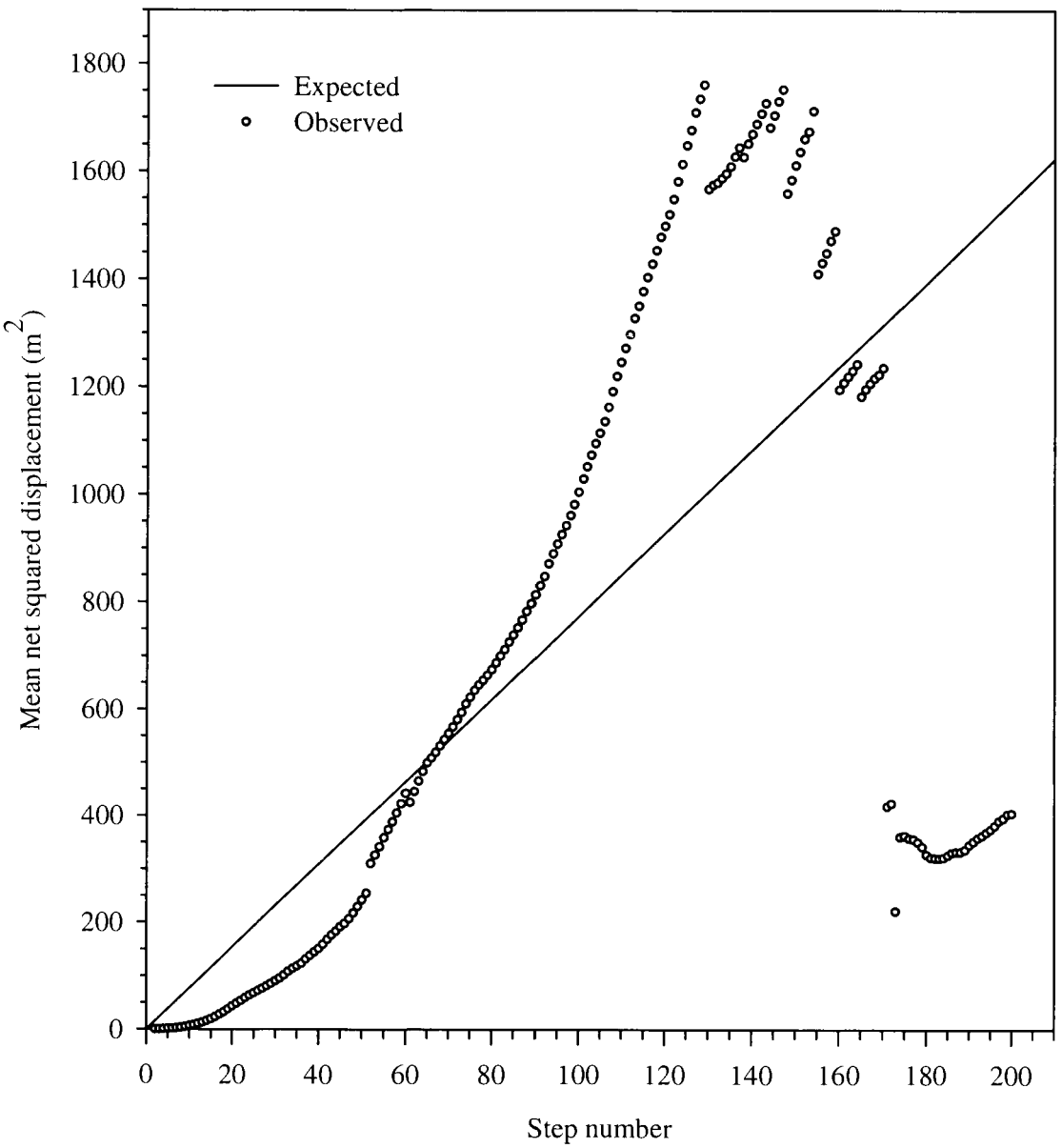

FIG. 26.—Observed (symbols) and predicted (solid line) mean net squared displacement of 15 male *Phrynosoma mcallii* pathways collected on the Barry M. Goldwater bombing range, near Yuma, AZ, during the summer of 2000.

Fractal Dimension

Among lizards observed during 2000 on the BMGR, the 10 female *P. mcallii* pathways had an average fractal dimension of 1.0858 and the 15 male *P. mcallii* pathways had an average fractal dimension of 1.0831. Among those flat-tailed horned lizards observed during 2000 on the NAF El Centro, the 10 females had an average fractal dimension of 1.0712 and the 15 males had an average fractal dimension of 1.0395 (Fig. 27). Significant differences were found among the pathways of those 25 individuals from BMGR and the 25 individuals from NAF El Centro ($F_{3,50} = 10.00$; $P < 0.0001$). Further, *a posteriori* tests indicated that the average fractal dimensions of *P. mcallii* males from NAF El Centro were significantly less than *P. mcallii* females from BMGR ($P < 0.05$), and NAF El Centro ($P < 0.05$) and *P. mcallii* males from BMGR ($P < 0.05$).

The fractal dimensions of *P. mcallii* pathways collected from BMGR and NAF El Centro during the 2000 field season were compared with *P. mcallii* pathways collected from the three treatment plots during the 1999 field season. Differences in the average fractal dimension between these groups were detected ($F_{9,106} = 2.56$; $P = 0.01$). Further, *a posteriori* analysis revealed one significant difference. The average fractal dimensions of male *P. mcallii* pathways from NAF El Centro during 2000 were significantly smaller than female *P. mcallii* pathways collected from the Sandy treatment during 1999 ($P = 0.02$).

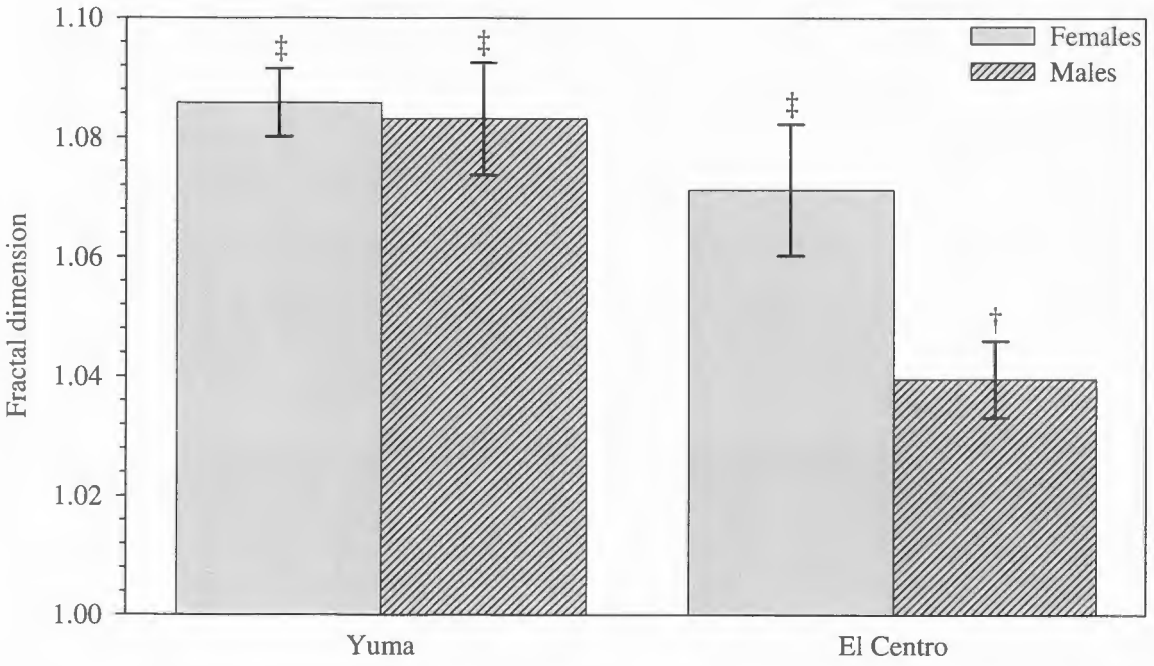

FIG. 27.—Average fractal dimension of 25 (10 female;15 male) Yuma and 25 (10 females; 15 males) El Centro *P. mcallii* pathways collected during the 2000 field season. Error bars equal ± 1 SE. Bars with different symbols denote significant differences ($P < 0.05$) in mean fractal dimensions.

DISCUSSION

Any number of reasons may explain why animals move within a given habitat. Searching for mates and food resources or avoiding predators are but a few factors important to most animals. Fisher et al. (2002) observed a variety of factors within and among sites correlated with the presence and abundance of coastal horned lizards. A mechanistic analysis of the movement patterns of individual lizards may provide insights into those factors determining habitat preference. The present study tested such a factor likely to be important for individual horned lizards under natural conditions. For the current study I was interested in how ecologically similar species are able to occupy similar habitats. Based on preliminary observation I hypothesized that these two species of sympatric horned lizards partitioned available habitat based on soil substrate texture.

Lizards were fitted with backpacks containing bobbins of thread and movement patterns were observed. Stress associated with capture and backpack attachment may have had some affect on the observed movement. Furthermore, the backpacks themselves may have altered the natural movement patterns of these lizards. These constraints, however, were held constant for each lizard and across both field seasons. Therefore, the capture effect was presumably consistent among all individuals

The simplest index for insights on how animals may be utilizing available habitat is to examine the net displacements of movement pathways. It is assumed that individuals who interpret a given habitat as satisfactory may walk a long distance but relative to their start position may actually displace themselves a much shorter distance. Conversely, assuming individuals who view a given habitat as unsatisfactory may move a

long distance which is similar to the actual displacement distance for its point of origin. With (1994) investigated the effects of habitat heterogeneity on the net displacement of three grasshopper species of different sizes. She observed a decrease in pathway net displacements as heterogeneity in heavily grazed pastures increased. Similarily, With et al. (1999) utilized the net displacement of common cricket (*Acheta domestica*) pathways to investigate movement responses to patch structure. As habitat variable (% grass) increased, crickets showed a decrease in net displacement. Furthermore, among smaller crickets the effect was more pronounced. These results were both interpreted as the individuals scaling the landscape mosaic of differing habitats differently.

During the summer of 1999 I set up an experiment to test if two similar species of horned lizards interpreted habitats varying in soil texture differently. Because *P. mcallii* appeared to be associated with sandy soils, I hypothesized that *P. mcallii* would view habitats with sandy substrates as optimal and landscapes with compact hard-pan substrates as suboptimal. Conversely because *P. platyrhinos* appeared to be associated with more hard-pan substrates, I predicted that *P. platyrhinos* would prefer a hard-pan substrate over a loose, fine, sand substrate. Movement pathways of 22 *P. mcallii* and 22 *P. platyrhinos* in three treatments with differing soil substrates showed no differences in the pattern of their pathways. Both *P. mcallii* and *P. platyrhinos* were equally as likely to move similar net displacements regardless of the structure of the soil substrate. However, the similarity in displacements of *P. mcallii* across treatments may have been affected by being translocated to unfamiliar landscapes. During the summer of 2000 I observed the movement pathways of an additional 25 *P. mcallii* from the BMGR, and 25 *P. mcallii*

from the Imperial Valley on the NAF El Centro, California. None of these individuals was translocated to the treatment plots used the year before. Movement pathways were collected from each lizard's original capture location. The same trends in movement patterns were observed. *Phrynosoma mcallii* individuals were just as likely to move similarly when transplanted to treatment with differing soil substrates as individuals who were on "familiar" habitats from two different populations.

Possibly a more robust index for interpreting animal pathways is to compute the fractal dimension of those pathways. The fractal dimension indexes the amount of tortuosity of a movement pathway. Therefore, following the same argument used for net displacements, it was assumed that an individual who views a habitat as satisfactory may transverse the habitat more thoroughly, resulting in a more tortuous pathway. Conversely, it is assumed that an individual who interprets a given landscape as sub-optimal may want to exit that habitat with a minimum amount of effort and therefore exhibit a more linear, i.e., less tortuous, pathway. Crist et al. (1992) observed that differences in vegetative cover or degree of grazing intensity did not have any affect on the fractal dimensions of movement pathways of three closely related species of darkling beetles (*Eleodes* spp.), despite size differences between the species. The similarity of the fractal structure of the movement pathways suggest the movement responses of these closely related species to varying heterogeneity, occupy the same domain of scale. However, With (1994) observed differences in fractal dimensions from pathways of three grasshopper species of varying size. The movement pathways of the two smaller species were significantly more tortuous than those of the single larger species, irrespective of the microhabitat structural complexity. These observations were interpreted as the larger

grasshopper species interacting within the habitat structure differently from the two smaller species. Furthermore, the fractal dimensions of the two smaller species were similar. These two species were interacting similarly with microhabitat structure. Because the two smaller species exhibited significantly greater fractal dimensions, they may be interacting with patch structure at a finer resolution than the larger grasshopper species. Differences in fractal dimension were also observed from cricket pathways recorded in landscapes differing in the degree of vegetative cover. Pathways collected from "non-vegetated" and "less-vegetated" landscapes were less tortuous than landscapes with greater percentages of grass cover (With et al., 1999).

Initial analysis of the 22 *P. mcallii* and 22 *P. platyrhinos* pathways from the treatments varying in substrate texture indicated no difference in fractal dimension between either horned lizard species or any of the treatments. Closer examination indicated that the fractal dimensions of female *P. platyrhinos* pathways, collected in the treatment with a hard-pan substrate, were significantly less tortuous that pathways of female *P. mcallii* from the sandy soil treatment and pathways of male *P. mcallii* from the intermediate soil texture treatment. This may indicate that female *P. platyrhinos* may be viewing the habitat with hard-pan substrates at a larger scale than female *P. mcallii* inhabiting sandy and male *P. mcalli*i inhabiting intermediate substrates. Fractal dimensions of pathways from individuals who were not translocated to "unfamiliar" habitats also differed. The pathways of male *P. mcallii* observed at NAF El Centro were significantly more linear than both female and male *P. mcallii* pathways collected on the BMGR from "familiar" landscapes and female *P. mcallii* pathways also collected on the BMGR from an "unfamiliar" sandy soil landscape. Again this could indicate that male *P.*

mcallii from "familiar" habitats at the NAF view their habitats at a larger scale than male and female *P. mcallii* from "familiar" habitats on the BMGR and *P. mcallii* females from "unfamiliar" sandy habitats.

A differing perspective to interpret movement patterns may be to compare observed pathway displacement to that expected as predicted by a correlated random walk model. A CRW model makes predictions about an individual's net squared displacement. Following the same assumptions before, if an individual views a habitat as satisfactory, its movement pathway and net squared displacement may approach or even be less than that predicted by a CRW model. On the other hand, if an individual interprets a habitat as suboptimum, then the quickest way to exit the habitat is to move in a more linear pathway, resulting in a greater net squared displacement than predicted by a CRW model. Kareiva and Shigesada (1983) were the first to compare expected net squared displacements of pathways to observed real data sets. They observed the flight pathways of cabbage white butterflies (*Pieris rapae*), while ovipositing in a collard garden, were remarkably well-described by a simple correlated walk model. However, while nectar-feeding in a field of goldenrods, the CRW model significantly under-predicted the observed displacement. While investigating harvester ant foraging movements, Crist and MacMahon (1991) compared the expected and observed net squared displacements of ants searching for food and ants running along trunk trails. For running ants, the CRW model significantly underpredicted ants net squared displacement. Intuitively this makes sense because the ants were not engaging in a random walk, but rather running along linear trails. The displacement of searching ants was more complex. In six out of 20 time steps the observe displacement diverged from the expected. This

departure came around moves 5–10, and after that the observed converged to the expected curve. Bergman et al. (2000) observed the movement patterns of migratory and sedentary Caribou (*Rangifer tarandus*) in north eastern Canada. Although observed annual squared displacements did not show a linear relationship with number of moves, contrary to the model predictions, the CRW modeled movements very well for up to 7 months for migratory caribou and for up to 3 months for sedentary caribou. These studies suggest that differing behaviors or temporal conditions can affect movement patterns.

Among the 22 *P. mcallii* and 22 *P. platyrhinos* observed from the differing soil treatments only one group of lizards pathways were similar to that predicted by a CRW model. The 11 male *P. platyrhinos* pathways observed within the hard-pan substrate treatment were similar to that predicted by a CRW model. In all other cases, regardless of species, sex, or treatment the CRW model clearly underpredicted the actual observed lizards net squared displacement. Those results indicate, in most cases, all lizards were moving in a more linear and directed pattern than would be predicted if these lizards were moving according to the model of a CRW.

Less clear trends were noticed among pathways of lizards collected from "familiar" habitats. Net squared displacements of female *P. mcallii* pathways observed at NAF El Centro were over predicted by the model. However, it appears that the general trend is similar to that predicted by the CRW model and a few individuals with very tortuous pathways influenced the overall trend. For male *P. mcallii* pathways at NAF El Centro, the CRW model under-predicted the actual observed net squared displacement. Among female *P. mcallii* pathways observed from "familiar" habitats on the BMGR, the

CRW model underpredicted the observed net squared displacement. However, the general trend of these lizards was similar to that predicted by the model, and again a few individuals appear to be influencing the significant difference. The net squared displacement for male *P. mcallii* from "familiar" habitat on the BMGR was under-estimated by the model.

Little correlation in substrate texture and distribution of *P. mcallii* and *P. platyrhinos* was observed. Soil texture does not appear to be an important factor affecting the observed distribution of *P. mcallii* and *P. platyrhinos* on the BMGR. Similarities in the net displacement of both species of horned lizards in each of the three "unfamiliar" treatments and among "familiar" habitat suggests substrate composition has little effect in determining horned lizard distribution.

Fractal analysis revealed that *P. mcallii* and *P. platyrhinos* were interacting with the landscape structure in a functionally similar manner, as evidenced by the similar D values of their movement patterns within each of the three treatments. Furthermore, within each species, substrate texture had no effect on how males and females moved within the available habitat. The translocation of *P. mcallii* individuals into each of three treatment plots appeared to have little effect on the lizards' movement pattern. Pathways of *P. mcallii* were similar for individuals translocated to treatment plots and individuals that were released at a "familiar" site of capture.

Furthermore the net squared displacement of most lizard pathways was severely underpredicted by a CRW model. Most lizard groups of both species moved in a more linear direction than predicted by the model.

However, the initial observation of *P. mcallii* and *P. platyrhinos* segregating themselves among the habitat is still apparent. The question of what is causing this segregation still remains to be addressed further. Could other behavioral mechanisms be at the root of these species segregation? Are other abiotic factors affecting the observed horned lizard pattern? Angert et al. (2002) found evidence that thermal environments were of greater importance in determining lizard occurrence than microhabitat characteristics. Differences in water retention ability among soil types (McAuliffe, 1994) may contribute to horned lizard distribution.

Alternatively, given that *P. platyrhinos* and *P. mcallii* are sister species, possible phylogenetic histories may constrain how these species interact with the substrate. Vitt et al. (2000) observed that closely related, morphologically similar species often exhibited similarities in microhabitat preference.

LITERATURE CITED

Abramsky, Z. and C. Sellah. 1982. Competition and the role of habitat selection in *Gerbillus allenbyi* and *Meriones tristrami*: a removal experiment. Ecology 63:1242–1247.

Anderson, D. J. 1983. Optimal foraging and the traveling salesman. Theoretical Population Biology 24:145–159.

Angert, A., L. D. Hutchison, D. Glossip, and J. B. Losos. 2002. Microhabitat use and thermal biology of the collard lizard (*Crotaphytus collaris collaris*) and the fence lizard (*Sceloporus undulates hycinthinus*) in Missouri glades. Journal of Herpetology 36:23–29.

Arlettaz, R., N. Perrin, and J. Hausser. 1997. Tropic resource partitioning and competition between the two sibling bat species *Myotis myotis* and *Myotis blythii*. Journal of Animal Ecology 66:897–91.

Beauchamp, B., B. Wone, S. Bros, and M. Kutilek. 1998. Habitat use of the flat-tailed horned lizard (*Phrynosoma mcallii*) in a disturbed environment. Journal of Herpetology 32:210–216.

Bell, W. J. 1991. Searching Behaviour: The Behavioural Ecology of Finding Resources. Chapman and Hall, London, U.K.

Bergman, C. M., J. A. Schaefer, and S. N. Luttich. 2000. Caribou movement as a correlated random walk. Oecologia 123:364–374.

Case, T. J. 1979. Character displacement and coevolution in some *Cnemidophorus* lizards. Fortschritte der Zoologie 25:235–282.

Case, T. J. 1983. Sympatry and size similarity in *Cnemidorophorus*. Pp. 297–325. *In* R. B. Huey, E. R. Pianka and T. W. Schoener (Eds.), Lizard Ecology: Studies of a Model Organism. Harvard University Press, Cambridge, Massachusetts, U.S.A.

Case, T. J. 1990. Patterns of coexistence in sexual and asexual species of *Cnemidophorus* lizards. Oecologia 83:220–227.

Claussen, D. L., M. S. Finker, and M. M. Smith. 1997. Thread trailing of turtles: methods for evaluating spatial movements and pathway structure. Canadian Journal of Zoology 75:2120–2128.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42:710–723.

Crist, T. O. and J. A. MacMahon. 1991. Individual foraging components of harvester ants: movements patterns and seed patch fidelity. Insectes Sociaux 38:379–396.

Crist, T. O., D. S. Guertin, J. A. Weins, and B. T. Milne. 1992. Animal movement in heterogeneous landscapes: an experiment with *Elodes* beetles in shortgrass prairie. Functional Ecology 6:536–544.

Dicke, M. and P. A. Burrough. 1988. Using fractal dimensions for characterizing the tortousity of animal trails. Physiological Entomology 13:393–398.

Dunham, A. E. 1980. An experimental study on interspecific competition between the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus*. Ecological Monographs 50:309–330.

Fair, W. S. and S. E. Henke. 1999. Movements, home ranges and survival of the Texas horned lizard (*Phrynosoma cornutum*). Journal of Herpetology 33:517–525.

Fisher, M., and A. Muth. 1995. A backpack method for mounting radio transmitters to small lizards. Herpetological Review 23:139–140.

Fisher, R. N., A. V. Suarez, and T. J. Case. 2002. Spatial patterns in the abundance of the coastal horned lizard. Conservation Biology 16:205–215

Funk, R. S. 1981. *Phrynosoma mcallii* (Hallowell) Flat-tailed horned lizard. Catalogue of American Amphibians and Reptiles 281:1–2.

Glazier, D. S. and S. E. Eckert. 2002. Competitive ability, body size and geographical range size in small mammals. Journal of Biogeography 29:81–92.

Grover, M. C. 1996. Microhabitat use and thermal ecology of two narrowly sympatric *Sceloporus* lizards. Journal of Herpetology 30:152–160.

Hairston, N. G. 1980a. The experimental test on an analysis of field distributions: competition in terrestrial salamanders. Ecology 61:817–826.

Hairston, N. G. 1980b. Evolution under interspecific competition. Field experiments on terrestrial salamanders. Evolution 34:409–420.

Hairston, N. G. 1987. Community Ecology and Salamander Guilds. Cambridge University Press, Cambridge, U.K.

Heath, J. E. 1965. Temperature regulation and diurnal activity in horned lizards. University of California Publications in Zoology 64:97–135.

Howard, C. W. 1974. Comparative reproductive ecology of horned lizards (Genus *Phrynosoma*) in Southwestern United States and Northern Mexico. Journal of the Arizona Academy of Science 9:108–116.

Irschick, D. J. and J. B. Losos. 1999. Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean Anoles. American Naturalists 145:293–305.

James, C. D. 1994. Spatial and temporal variation in structure of a diverse lizard assemblage in arid Australia. Pp. 287–317. *In* Lizard Ecology: Historical and Experimental Perspectives. L. J. Vitt and E. R. Pianka (Eds.). Princeton University Press, Princeton, New Jersey, U.S.A.

Johnson, A. R., J. A. Wiens, B. T. Milne, and T. O. Crist. 1992. Animal movements and population dynamics in heterogeneous landscapes. Landscape Ecology 7:63–75.

Johnson, R. A. 1992. Soil texture as an influence on the distribution of the desert seed-harvester ants *Pogonomyrmex rugosus* and *Messor pergandei*. Oecologia 89:118–124.

Kareiva, P. M. and G. Odell. 1987. Swarms of predators exhibit preytaxis if individual predators use area restricted search. American Naturalist 130:233–270.

Kareiva, P. M. and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. Oecologia 56:234–238.

Lewin, R. 1983. Santa Rosalia was a goat. Science 221:636–639.

Losos, J. B. 1994. Historical contingency and lizard community ecology. Pp. 319–333. *In* Lizard Ecology: Historical and Experimental Perspectives. L. J. Vitt and E. R. Pianka, (Eds.). Princeton University Press, Princeton, New Jersey, U.S.A.

MacArthur, R. 1970. Species packing and competitive equilibrium for many species. Theoretical Population Biology 1:1–11.

MacMahon, J. A., J. F. Mull, and T. O. Crist. 2000. Harvester ants (*Pogonomyrmex spp.*): their community and ecosystem influences. Annual Review of Ecology and Systematics 31:265–291.

Mandelbrot, B. B. 1983. The fractal geometry of nature. Freeman, San Francisco, California, U.S.A.

McAuliffe, J. R. 1994. Landscape evolution, soil formation, and ecological patterns and processes in Sonoran desert bajadas. Ecological Monographs 64:111–148.

McCulloch, C. E. and M. L. Cain. 1989. Analyzing discrete movement data as a correlated random walk. Ecology 70: 383–388.

Milne, B. T. 1991. Lessons from applying fractal models to landscape patterns. Pp. 199–235. *In* Quantitative Methods in Landscape Ecology. M. G. Turner and R. H. Gardner (Eds.). Springer-Verlag, New York, New York, U.S.A.

Milne, B. T. 1997. Applications of fractal geometry in wildlife biology. Pp. 32–69. *In* Wildlife and Landscape Ecology Effects of Pattern and Scale. J. A. Bissonettee (Ed.). Springer-Verlag, New York, New York, U.S.A.

Montanucci, R. R. 1987. A phylogenetic study of the horned lizards, genus *Phrynosoma*, based on skeletal and external morphology. Contributions in Science 390:1–36.

Morin, P. J. 1986. Interactions between intraspecific competition and predation in an amphibian predator-prey system. Ecology 67:713–720.

Nams, V. O. 1996. The Vfractal: a new estimator for fractal dimension of animal movement paths. Landscape Ecology 11:289–297.

Norris, K. S. 1949. Observations on the habits of the horned lizard *Phrynosoma m'callii*. Copeia 1949:176–180.

Pacala, S. and J. Roughgarden. 1982. Resource partitioning and interspecific competition in two two-species insular *Anolis* lizard communities. Science 217:444–446.

Pacala, S. and J. Roughgarden. 1985. Population experiments with *Anolis* lizards of St. Maartenand St. Eustatius. Ecology 66:129-–141.

Peters, R. H. 1983. The Ecological Implications of Body Size. Cambridge University Press, Cambridge, U.K.

Petren, K. and T. J. Case. 1998. Habitat structure determines competition intensity and invasion success in gecko lizards. Proceedings of the National Academy of Sciences USA 95:11739–11744.

Pianka, E. R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics. 4:53–74.

Pianka, E. R. 1986. Ecology and Natural History of Desert Lizards: Analysis of the Ecological Niche and Community Structure. Princeton University Press, Princeton, New Jersey, U.S.A.

Pianka, E. R., and W. S. Parker. 1975. Ecology of horned lizards: a review with special reference to *Phrynosoma platyrhinos*. Copeia 1975:141–162.

Pyke, G. H. 1984. Animal movements: an optimal foraging approach. Pp. 7–31. *In* I. R. Swingland and P. J. Greenwood (Eds.), The Ecology of Animal Movement. Claredon Press, Oxford, U.K.

Radtkey, R. R., S. M. Fallon, and T. J. Case. 1997. Character displacement in some *Cnemidophorus* lizards revisited: a phylogenetic analysis. Proceedings of the National Academy of Sciences USA 94:9740–9745.

Reeve, W. L. 1952. Taxonomy and distribution of the horned lizard genus *Phrynosoma*. University of Kansas Scientific Bulletin 34:817–960.

Robinson, S. K. and J. Terborgh. 1995. Interspecific aggression and habitat selection by Amazonian birds. Journal of Ecology 64:1–11.

Root, B. R. and P. M. Kareiva. 1984. The search for resources by cabbage butterflies (*Pieris rapae*): ecological consequences and adaptive significance of markovian movements in a patchy environment. Ecology 65:147–165.

Rorabaugh, J. C., C. L. Palermo, and S. C. Dunn. 1987. Distribution and relative abundance of the flat-tailed horned lizard (*Phrynosoma m'callii*) in Arizona. Southwestern Naturalist 32:103–109.

Schoener, T. W. 1983. Field experiments on interspecific competition. American Naturalists 122:240–285.

Scudday, J. F. and J. R. Dixon. 1973. Diet and feeding behavior of the teiid lizards from trans-Pecos Texas. Southwestern Naturalists 18:279–289.

Smith, D. C. 1981. Competitive interactions of the plateau lizard (*Sceloporus virgatus*) and the tree lizard (*Urosaurus ornatus*). Ecology 62:679–687.

Stebbins, R. C. 1985. A Field Guide to Western Reptiles and Amphibians. Houghton Mifflin Company, Boston, Massachusetts, U.S.A.

Swihart, R. K., N. A. Slade, and B. J. Bergstorm. 1988. Relating body size to the rate of home range use in mammals. Ecology 69:393–399.

Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the special distribution of foragers. Ecology 72:1253–1266.

Turchin, P. 1998. Quantitive Analysis of Movement: Measuring and Modeling Population redistribution in Animals and Plants. Sinauer Associates, Sunderland Massachusetts, U.S.A.

Turner, F. B., and P. A. Medica. 1982. The distribution and abundance of the flat-tailed horned lizard (*Phrynosoma m'callii*). Copeia 1982:815–823.

United States Department of Agriculture. 1941. Climate and Man Yearbook of Agriculture. United States Government Printing Office, Washington DC, U.S.A

Vitt, L. J., T. C. S. Avila-Pires, J. P. Caldwell, and V. R. L. Oliveira. 1998. The impact of individual tree harvesting on the thermal environments of lizard in Amazonian rain forest. Conservation Biology 12:654–664.

Vitt, L. J., S. S. Sartorius, T. C. S. Avila-Pires, M. C. Esposito, and D. B. Miles. 2000. Niche segregation among sympatric Amazonian teiid lizards. Oecologica 122:410–420.

Wiens, J. A. 1977. On competition and variable environments. American Scientists 65:590–597.

Wiens, J. A. 1990. On the use of 'grain' and 'grain size' in ecology. Functional Ecology 4:720.

Wiens, J. A., T. O. Crist, K. A. With, and B. T. Milne. 1995. Fractal patterns of insect movement in microlandscape mosaics. Ecology 76:663–666.

Wiens, J. A. and B. T. Milne. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetles' perspective. Landscape Ecology 3:87–96.

Wilson, D. S. 1994. Tracking small animals with thread bobbins. Herpetological Review 25:13–14.

With, K. A. 1994. Using fractal analysis to assess how species perceive landscape structure. Landscape Ecology 9:25–36.

With, K. A., s. J. Cadaret, and C. Davis. 1999. Movement responses to patch structure in experimental fractal landscapes. Ecology 80:1340–1353.

Zamudio, K. R. and G. Parra-Olea. 2000. Reproductive mode and female reproductive cycles of two endemic Mexican horned lizards (*Phrynosoma taurus* and *Phrynosoma braconnieri*). Copeia 2000:222–229.

Zar, J. H. 1999. Biostatistical Analysis, 4th ed. Prentice Hall, Englewood Cliffs, New Jersey, U.S.A.

CURRICULUM VITAE

DANIEL H. FOLEY III

PERSONAL INFORMATION

Born: 25 June 1969, Lubbock, Texas
Social Security Number: 465-65-4133
Married; no children

OFFICE ADDRESS:
Department of Biology
Utah State University
Logan, Utah 84322-5305
Telephone: (435) 797-2450
FAX: (435) 797-1575
e-mail: wildlife@biology.usu.edu

HOME ADDRESS:
188 West 400 South
Logan, Utah 84321
Telephone: (435) 753-5997

EDUCATION

Bishop Lynch High School
Dallas, Texas (1984–1987)

BS, Wildlife & Fisheries Sciences, Texas A&M University
College Station, Texas (1987–1991)

MS, Wildlife & Fisheries Sciences, Texas A&M University
College Station, Texas (1991–1994)
Thesis: Short-term response of herpetofauna to timber harvesting in conjunction with streamside-management zones in seasonally-flooded bottomland-hardwood forests of southeast Texas.
Advisor: Dr. James R. Dixon

Ph.D., Department of Biology, Utah State University
Logan, Utah (1997–2002)
Dissertation: Movement patterns of *Phrynosoma mcallii* and *Phrynosoma platyrhinos* in response to substrate texture.
Advisor: Dr. Edmund D. Brodie, Jr.

EMPLOYMENT

Herpetologist (1995-1997)

Maryland Department of Natural Resources -- Investigated the effectiveness of two different survey techniques (drift fence and time-constrained searches) for deducing amphibian and reptile distributions and abundance within the state of Maryland.

Teaching Experience

Public Speaker: Numerous presentations (ca. 30) on natural history of amphibian and reptiles to schools, community and nature groups.

Graduate Teaching Assistant: Department of Wildlife & Fisheries Sciences, Texas A&M University (1991)

Herpetology (1 semester)

Field Herpetology (1 semester)

Graduate Teaching Assistant: Department of Biology, Utah State University (1998-2002)

Field Ecology (1 semester)

Introductory Biology I (2 semesters)

Introductory Biology II (2 semesters)

Human Physiology (3 semesters)

RESEARCH

RESEARCH INTERESTS

Behavioral ecology and natural history of vertebrates; special interest on amphibians and reptiles. Affects of land use patterns on local vertebrate populations. Mechanisms of species packing and ecological niche differentiation. Wildlife management of native Texas game species specifically upland game birds.

FIELD EXPERIENCE

Central Texas (1991)

Field work along the Colorado and Conch rivers conducting a long term study of three sympatric species of water snakes (*Nerodia erythrogaster*, *N. harteri*, & *N. rhombifer*).

Central Texas (1993)

Conducted surveys for endangered Houston toads (*Bufo houstensis*)

Australia (1993)

One month traveling the northern, eastern and southern portions of the country observing and photographing wildlife.

East Texas (1991-1994)

Investigated the effects of several timber harvesting practices on local amphibian and reptile populations.

Maryland (1994-1997)

Conducted distributional surveys for amphibians and reptiles throughout the state.

Costa Rica (1995)

One month of field work assisting in satellite telemetry of leatherback sea turtles (*Dermochelys coriacea*).

Nevada (1997)

Three months collecting distributional and ecological data of chuckwallas (*Sauromalus obesus*)

Madagascar (1998-1999)

Four months of field work conducting amphibian and reptile surveys of several remote locales.

Guatemala and Nicaragua (1999)

One month conducting amphibian and reptile surveys of several remote locales.

Southwestern United States (Arizona, California; 1999-2000)

Two summers collecting distributional and ecological data on horned lizards (*Phrynosoma mcallii* and *P. platyrhinos*)

PUBLICATIONS (all refereed)

1. **Foley, D.H., III**. 2002. Notes on the effects of a *Trimorphodon biscutatus* bite on a human. Herpetological Review. *In Press.*
2. **Foley, D.H., III**. 2002. Field observations on the movements and behavior of the Malagasy leaf chameleon *Brookesia therezieni* (Squamata: Chameleonidae). Herpetological Natural History. *In Press.*

MANUSCRIPTS SUBMITTED

3. FOLEY, D.H., III AND S.A. SMITH. Herpetofauna inventory methods: drift fence versus time-constrained searches. Journal of Wildlife Management (12 ms pp.)
4. Gardner, T.J., **D.H. Foley III**, K.V. Young, and E.D. Brodie, Jr. The use of barrier fences to prevent road mortalities in the flat-tailed horned Lizard (*Phrynosoma mcallii*). Wilson Society Bulletin (9 ms pp.)

MANUSCRIPTS IN PREPARATION

5. **Foley, D.H., III**. Does soil texture affect the distribution of *Phrynosoma mcallii* and *Phrynosoma platyrhinos*?
6. **Foley, D.H., III**. A modified back-pack design for attaching spools of thread to lizards.
7. **Foley, D.H., III**. and J. R. Dixon. Herpetofauna response to timber harvesting practices in seasonally flooded bottomland hardwood forests of southeast Texas.

REPORTS

1. **Foley, D.H., III** and S.A. Smith. 1999. Comparison of two herpetofaunal inventory methods and an evaluation of their use in a volunteer-based statewide reptile and amphibian atlas project: final report. USGS Cooperative agreement No. 1445-CA-09-95-0029. 68 pp.
2. Gardner, T.J. and **D.H. Foley III**. 2001. Final Report: Survey for Flat-tailed Horned Lizards, *Phrynosoma mcallii*, at the Naval Air Facility, El Centro, California, U.S. Navy Agreement No. N68711-98-LT-80030. 55 pp.
3. Gardner, T.J., Young, K.V., **D.H. Foley, III**. 2001. Final report: management-based study of the flat-tailed horned lizard, *Phrynosoma mcallii*. U.S. Bureau of Reclamation Grant Agreement No. 00FG340008. 47 pages.

PRESENTATIONS

"Effects of timber harvesting with streamside management zones on herpetofauna inhabiting seasonally flooded bottomland hardwood forests in southeast Texas"

Joint meeting of the Herpetologists' League and Society for the Study of Amphibian and Reptiles, University of Georgia, Athens, Georgia (July 1994).

"Determining herpetofaunal species composition: terrestrial drift fence sampling vs. time-constrained searches"

Annual Meeting of the Society for the Study of Amphibians and Reptiles, Appalachian State University, Boone, North Carolina (August 1995).

"Herpetofauna inventory methods: Drift fences vs. time-constrained searches"

Joint meeting of the American Society of Ichthyologists and Herpetologists and Herpetologists' League, New Orleans, Louisiana (July 1996).

"Notes on the daily movements, roosting, and home range of the Malagasy leaf chameleon *Brookesia therezieni*"

Joint meeting of the American Society of Ichthyologists and Herpetologists, American Elasmobranch Society, Herpetologists' League and Society for the Study of Amphibians and Reptiles, The Pennsylvania State University, State College, Pennsylvania (June 1999).

PROFESSIONAL AFFILIATIONS

The Southwestern Association of Naturalists

Society for the Study of Amphibians and Reptiles

Herpetologists' League

Texas Herpetological Society

Wildlife Biology Society

Member of The Declining Amphibian Populations Task Force Southern Plains Working Group